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Socio-sexual behaviour in two groups of captive Bonobos (*Pan paniscus*): a description and functional analysis

By Peter A. Brown

Biological Anthropology MSc

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University of Durham

Department of Anthropology

Supervisor: Dr J deRuiter



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Socio-sexual behaviour in two groups of captive Bonobos (*Pan paniscus*): a description and functional analysis

By Peter A. Brown

“This dissertation is the result of my own work. Material from the published or unpublished work of others, which is referred to in the dissertation, is credited to the author in the text. The dissertation is approximately 40,000 words in length”.

Abstract

This study is an investigation into bonobo socio-sexual behaviour in two captive groups, Twycross in Leicestershire and Planckendael in Belgium. There are four main areas of emphasis and these are reconciliation, tension reduction, social bonding and social status affirmation, which formed the four hypotheses. Both study groups had a similar range, frequency and distribution of socio-sexual behaviour across the sexes and ages. Differences were apparent both within each group and between them and also comparing data from other captive and wild studies. Socio-sexual behaviour occurs in many species, but it is the range of socio-sexual behaviour, frequency, and combinations of age and sex that are specific to bonobos.

Quantitative data on socio-sexual behaviour were collected using all occurrences and scan sampling techniques, to test the hypotheses using SPSS for windows. The four hypotheses tested are as follows: Hypothesis I: Reconciliation is in the form of socio-sexual behaviours. Hypothesis II: Socio-sexual behaviours are a form of tension reduction. Hypothesis III: Socio-sexual behaviours are an expression of social status. Hypothesis IV: Social bonding is increased by the occurrence of frequent genital contacts.

Results indicate that of the four hypotheses tested, two were relatively strongly supported by the data; these were tension reduction and social status affirmation. Of these, the evidence for tension reduction was the strongest. The hypothesis for reconciliation was not supported by the data, but the social bonding hypothesis was partially supported. Socio-sexual behaviour was particularly evident during feeding and agonistic interactions (although agonism frequency was low). Rank related sexual

position, with dominant individuals as mounter and initiator, supported the social status hypothesis.

The difficulties of studying functions in captivity have been discussed in this study, but also the benefits compared to studies undertaken in the wild. These include a more detailed analysis, the greater knowledge of kin and social relationships and also that observations can be conducted in the presence of a more 'controlled environment', justify studying function in captivity to complement results from wild studies.

Acknowledgements

Firstly I must thank the staff at Twycross Zoo. In particular the bonobo keeper Marcus Smith, for his invaluable information and cooperation with the study group and also the research officer, Joanna Baker, without whom this study would not have been possible. Secondly I must thank Planckendael Zoological Park, Mechelen, Belgium. In particular Linda van Elsacker, Mieke de Lathouwers and Birgen Meuleman for their invaluable assistance and information.

I must also thank my dissertation tutor; Dr Jan de Ruiter for his advice and support throughout the study, also to colleague, Richard Marvan. Last, but not least, a big thank you to Bob Williams and his endless knowledge of SPSS and statistical analysis.

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I will briefly describe the characteristics and behaviour of bonobos (*Pan pansicus*) and the theories and data relating to socio-sexual behaviour that explain this behaviour in relation to reconciliation, tension reduction, social status and social bonding. This overview will include discussing data from both captive and wild groups and comparing these data to other species including other primates and especially the other *Pan* species; the chimpanzee (*Pan troglodytes*). Such a study is important from an anthropological perspective because the two *Pan* species are our closest living relatives and thus provide the opportunity to compare aspects of the behaviour across species. Such comparisons have been made with good results (Tinbergen 1963). In this thesis I will restrict myself to comparison of close relatives, where the issue of evolutionary divergence is less relevant (Harvey & Pagel 1998). I will start with a description of bonobo biology, including physical and social aspects, followed by socio-sexual behaviour and the theories and data surrounding this, together with dominance, reconciliation and tension reducing mechanisms.

1.1 Bonobo biology including social structure

The bonobo is the least studied of the four great ape species. This is partly because their range is very limited. Bonobos occur in the rainforest of the Congo, south of the Zaire River, east to west for 900km and north to south for 600km, and this area is very inaccessible (Kano 1992:41). Also it may possibly be partly due to the fact that, for a long time, bonobos were seen as 'just' a different subspecies of chimpanzee (de Waal 1997). Consequently, bonobos were not seen as important to study in their own right, and chimpanzees were much more accessible, due to a wider range from West to East Africa and varying habitats. Divergence between chimpanzees and bonobos (around 1.5 mya) is very recent on an



evolutionary timescale and therefore the two *Pan* species can be expected to be very similar in many respects (Morin et al 1994). However, there are many differences between the two species. The ecological niche for bonobos is more restricted whereas the chimpanzee occupies a wider range of habitats and is consequently more 'successful'. The ancestors of chimpanzees lived to the north of the Zaire River where greater climatic and environmental changes existed and this probably resulted in greater adaptability. The ancestors of bonobos were relatively restricted geographically and have remained in a fairly constant environment (Kano 1992:210, Morin et al 1994).

In 1978 Zihlman et al. undertook a comparative study of bonobo and *Australopithecine* morphology and found that measurements of bonobo skeletons produced results strikingly similar to dimensions of australopithecine skeletal material. Differences were suggested to relate to differing methods of locomotion: *Australopithecus* was bipedal and the bonobo is quadrupedal. This led to a claim that bonobos, while not ancestral to current panids and hominids were the best living model to serve as a 'proto-form' (Zihlman et al. 1978). Susman (1984) disagreed with this saying that bonobos derived from chimpanzees and were adapted to a tropical rainforest habitat. Blount (1990) supports Susman, suggesting that ecology is the most appropriate way to explain differences between chimpanzees and bonobos. The cladistic evidence from both DNA sequences and morphology demonstrate that the African apes (chimpanzees, bonobos and gorillas) are more closely related to humans than to the Asiatic apes (orang-utans and gibbons) and that chimpanzees are closer to humans rather than to gorillas (Goodman 1996, Shoshani et al. 1996, Page 2001:23). Thus, this view favours merging the traditional Pongidae and Hominidae into a single monophyletic family (Goodman 1996, Shoshani et al. 1996). Recent DNA evidence from Page et al. (2001) supports this, suggesting that the two species of chimpanzee form a strong clade with each other and also with their sister subgenus *Homo*, and together with the gorilla form the subtribe

Hominina (Page 2001:19). Chimpanzees and humans, who have their LCA (age of last common ancestor) 6 mya form a single genus *Homo*, humans in the subgenus *H. (Homo)* and chimpanzees and bonobos in the subgenus *H. (Pan)* (Page et al: 2001:23, Goodman et al 1998:596).

It was not until researchers Badrian and Badrian (1977), Kano (1980) and Nishida (1972) began observing bonobos that the enormous differences between the two *Pan* species became apparent, both physically and with respect to social behaviour and structure. Significant differences also exist between other closely related species such as the hamadryas (*Papio hamadryas*) and savannah baboon (*Papio cynocephalus*) and the stump-tail (*Macacca arctoides*) and rhesus macaque (*Macacca mulata*). For example, aspects of personalities, temperament and 'style' of dominance differ (Kummer 1975, Parish et al 2000:99). Parish and De Waal (2000) believe bonobos and chimpanzees have "some major important differences" (2000:105). They point out that, the use of contact aggression in inter-group interactions is rare in bonobos, but common in chimpanzees. Moreover, during inter-group encounters female bonobos may copulate with one or several males from the other group, even in the presence of the resident males. Such behaviour has never been observed in chimpanzees. Sexual behaviour in general is very different in the two species. In bonobos sexual behaviour is seen in a much wider variety of age/sex combinations and a much wider variety of non-reproductive contexts, for example, sexual behaviour between females, and between adults and juveniles (Parish & de Waal 2000:105, de Waal 2000, 1990, 1987, Kano 1992).

Physically chimpanzees are slightly stockier in build, more robust and with a larger skull. Bonobos, in contrast, are more slender in build, with smaller skulls and longer limbs, especially the legs, giving a more slim featured appearance overall. On average a bonobo is about 85% of the weight of a chimpanzee, but large differences occur between captive and

wild bonobos and chimpanzees and also between subspecies of chimpanzees (Kano 1994, Parish 1996). Chimpanzee females were found to be 84% the size of males (Uehara & Nishida 1987) and in humans this was 85% (Martin 1990). For bonobos Parish (1996) found that on average female bonobos were 82.5% the size of males, and females averaged 35.85kg and males 43.43kg (1996:81). Despite males having a considerable size and weight advantage they appeared not to use it in defence against females with female cooperation the main factor (1996:81).

With respect to social structure, both species form fission-fusion societies; subgroups move independent of one another, but converge periodically. The size and composition of such subgroups may vary over time. Adolescent females in both species leave their natal group to join a neighbouring group. The two species do differ, however, in the pattern of this fission-fusion. Bonobos form mixed parties of males, females and offspring, whereas chimpanzees have three possible kinds of parties often occurring simultaneously, all male, mother-offspring, and males/females who have no dependent offspring (Kano 1992:90 Wrangham 1993, White 1996:30, Vervaecke & Elsacker 2000:109). The degree to which females migrate varies enormously in chimpanzees from around 100% in Mahale (Tanzania) to around 15% in Gombe (Tanzania). It was until recently unknown to what extent female bonobos vary in migration patterns (Nishida et al 1990, Goodall 1986). However data from Gerloff et al. (1999) suggests that females disperse. In both societies males stay in their natal group (male philopatry) and this pattern of sex dependent dispersal has been confirmed through genetic analysis (Fedigan et al 1984, Takenaka et al 1993, Parish 1996, Gerloff et al. 1999).

Social bonding in both human and non-human primates, as in many other species, involves “positive” social relationships including affiliative interactions and cooperation over a long period of time and the strongest bonds are therefore most frequent between close

relatives (Walters & Seyfarth 1987, Parish 1996:62). This pattern concurs with kin selection theory, the inclusive fitness theory states that an individual can indirectly increase their own fitness by assisting genetic relatives in reproducing (Hamilton 1964). In bonobos, Kano (1992) describes three “unit groups”, according to how individuals are bonded, unlike “parties” as described previously where the bonding of these parties was not discussed. Kano’s “unit groups” consist of mother-offspring (the strongest bonded), adult males (both related and unrelated) and young adolescent females (the least bonded) (1992:76).

In primate species bonding generally is related to patterns of dispersal, with the philopatric sex invariably bonding much more strongly than the non-philopatric sex (Parish 1996:62, Wrangham 1980, de Waal 1982). Many multi-male multi-female primate groups have female philopatry (the males disperse and females stay in their natal group and are therefore closely related) such a pattern is termed ‘female bonded’ (Wrangham 1980). The great apes and probably humans show a different pattern. They generally show male philopatry. This has been related to the importance of male bonding in these ‘political’ species. Coalitions and complex alliance formations in male Chimpanzees are well documented (Goodall 1986, de Waal 1982). Female bonding may be expected to be weaker than for males (Wrangham 1980). Human females (*Homo sapiens sapiens*) are unusual in primates in that they do form bonds between non-related individuals. Hrdy (1981) showed that female primates have social strategies and are not sexually and socially passive, and that female social relationships have a great impact on group dynamics (Laland et al 2002:103). Smuts (1992) on the other hand argues however, that unrelated women in most human societies do not form such ‘coalitions’. She argues that rather they do not resist male aggression, despite female cooperation being an effective means to counteract this.

In bonobos, females have ‘a pattern of affiliation that is very unusual, if not unique, for a ‘non-female philopatric (non-female bonded) species’ (Parish 1996:72). Parish studied

'fishing behaviour' at artificial termite sites (for honey or milk powder) and found major differences between chimpanzees and bonobos. Chimpanzees had a more or less equal distribution of access and across both sexes. For bonobos, males fed for only 9% of the time they had access to the food, whereas chimpanzee males fed for 25% of the time. Monopolization of the feeding site by female bonobos was a key factor (1996:72). Priority of access and the length of time feeding were also dependent on the rank of the individual (also deduced from the results of agonistic interactions and displacements). Co-feeding was also higher among bonobos than chimpanzees, especially among females and led to monopolisation of the food source. Sexual interactions occurred in half of all the fishing bouts and often preceded co-feeding by the females, who despite being unrelated co-fed rather than competed, possibly suggesting socio-sexual behaviour is used to reduce tension, which I will be investigating in my research (Parish 1996:74/75).

Another important difference is that chimpanzees are a 'male dominated' society. Male chimpanzees form long-term relationships and coalitions with male relatives. Such long-term bonds are lacking among female chimpanzees, probably partly because they are immigrants to the group and therefore unrelated (Furuichi 1989, Idani 1991). Social relationships between adult female bonobos are especially strong and long lasting. This is despite the observations on female dispersal at puberty, where young females usually transfer into a new group alone and focus their attention to the older dominant females and not on other young females like themselves (Furuichi 1989, Idani 1991). Female bonobos with offspring have not been seen to transfer to other groups and those with sons probably stay in that group forming long-term bonds with sons throughout adulthood (Furuichi 1989, Kano 1992, Gerloff et al. 1999). Furuichi and Ihobe speculate that males born while their mothers were young are late adolescents when their mothers are in their prime and may have an increased chance to gain rapidly in rank because of this if their mothers are of high rank.

Males born to older mothers may have more difficulty as when they reach adulthood their mothers will probably be too old to support them in dominance relations (Furuichi 1997:870, Furuichi & Ihobe 1994:221).

For chimpanzees it is males who have elder brothers who are most likely to rise in rank at adulthood, with support of their male kin. Alpha male chimpanzees are usually at a prime adult age, whereas in bonobos it is the male's mother who is in her prime, he being much younger (Furuichi 1997:871). In female exogamous species, reproductive success is suggested to be separate from dominance rank (van Schaik 1989). Although Pusey (1997) found that in chimpanzees the higher the mothers rank the higher the infant survival, however with no matrilineal relationship in bonobos this is not possible to ascertain. Gerloff et al. (1999) undertook DNA analysis from faecal samples taken from the Eyengo community in Lomako. This was the first study to assess the relationship within a group of bonobos (1999:1192). The data supports that of female exogamy (Kano 1982; Furuichi 1989; Idani 1991; Hashimoto et al. 1996). Further evidence was found that for the majority of adult/subadult males there was a mother present in the group, but not for the females (Gerloff 1999:1192). Also the large range of 'mitochondrial haplotypes' suggests no matrilineal organization but a large exchange of females between groups (Gerloff et al. 1999:1192).

In the Eyengo community it was found that two high-ranking females did have a high survival/reproduction rate and two of their sons (in succession) became the dominant male and were responsible for the highest number of paternities (Gerloff 1999:1193). Evidence shows that these high-ranking males had the greatest reproductive success, but not necessarily the highest number of copulations. Dominant male chimpanzees have reproductive strategies that increase their chances of fertilization over those of lower ranking males (Tutin 1979, Goodall 1986). A male's reproductive success depends upon his influence over other males, cooperation with females and his use of agonism, affiliation and forced copulations (Tutin

1979, Goodall 1986). In bonobos mating is usually opportunistic, although whether this affects a male's chance of fertilization is not clear. Males do not disperse from their natal group; they stay with their mothers all their lives. Males have, therefore, strong life long lasting bonds with their mothers, who, moreover, support their sons in agonistic interactions. Consequently males, for the most part inherit their rank from their mothers (Kano 1992, Furuichi 1997:870, Furuichi & Ihobe 1994, Parish & de Waal 2000:100).

In summary bonobos have many similarities as well as differences with chimpanzees, both socially and physically. Similarities include both species are fission-fusion societies; have male philopatry and adolescent females leave their natal groups. Differences include the use of agonism and sexual behaviour, which are very different between the two species as are the 'bonding' patterns. Male agonism between male chimpanzees and against females is common, whereas bonobo males are much less agonistic towards each other and especially against females. Sexual behaviour in bonobos occurs in many forms and across all age/sex categories and a wide range of social situations, hence the term socio-sexual. For chimpanzees sexual behaviour is more limited in type, context and age/sex combinations. Bonobos are more slender in appearance with smaller skulls; chimpanzees are stockier and more robust. In bonobos females are dominant over males, a rarity among primates, male dominance, as seen with chimpanzees, is more common in many primate species. Lastly bonding differs between the two species chimpanzees exhibit male affiliation and form coalitions, while it is bonobo females who associate and form coalitions.

1.2 Dominance relationships

Parish et al (2000) note that there is a reluctance to accept female bonobo dominance by many scientists and researchers including Kuroda (1980) Kano (1992) Wrangham (1997) and Furuichi (1997) (2000:99). Furuichi recognises that female bonobos have a high social

status but still describes females as having “a dominance status comparable with males” (1997:856); Gerloff (1999) also stated that male and female bonobos at Lomako were “co-dominant” (1999:1194). Kano, who initially suggested males and females were more or less equal in dominance, now recognises that females dominate males in bonobo society. He makes an important point, namely that almost all agonistic interactions and dominance interactions occur around feeding. Kano also states that in all dominance interactions, no matter what context, “males submit to dominant females” (Parish et al 2000:101).

Barbara Fruth, cited in Parish et al. (2000) observed bonobos in the Lomako Forest, and also concluded that females dominate males. Fruth stated that, “Females show a high degree of association, form coalitions, and dominate the society” (Parish et al 2000:101).

Part of the problem regarding the reluctance to accept female dominance by some scientists is the historical and theoretical background, although now it is generally recognised that females are dominant in bonobo society (Kano 1992, Parish 1996, de Waal 1987, 1989, 1990, Vervaecke 2000) Evidence comes from observations both in captive and wild groups where females control food resources and may attack males who interfere with another female who is copulating (Kano 1992). Great apes have been classified as non-female bonded. An exception to this classification possibly exists in some societies of chimpanzees, societies like Gombe (Goodall 1986), Bonobos also appear to form an exception to this “rule”. Male-male relationships in bonobos do not have the close intimate bonds that chimpanzees have and bonobo males do not form coalitions. This is possibly unexpected because bonobo males like chimpanzee males are more closely related than the females (who transfer from other groups). (Parish et al 2000:101). The bonds between bonobo females facilitate close female cooperation and the ability to dominate males and prevent male intimidation, which is frequent in chimpanzees (Parish 2000:104).

1.3 Validity of comparison between apes and humans

Bonobos and chimpanzee studies on aspects of their biology, including behaviour can inform us on the human condition. Laland et al. (2002) highlight the “value of making comparisons across species”, saying this, caution is necessary as behaviours can appear to be similar in humans and other animals but are actually very different (2002:11). An example of particular relevance is male/male mounting, observed in many primate species including bonobos. This has been described as ‘homosexual behaviour’ (Bagemihl 1999, Takenoshita 1998:364, Yamagiwa 1987), although little research has been carried out to investigate whether this mounting in primates and human male homosexuality have “an identical proximate cause, life time development, function or evolutionary history” (Laland et al. 2002:11), Tinbergen’s (1963) four questions, see further below. This thesis tries to partially fill in the gaps. As Dixson (1998) suggests same sex mounting appears to be related to social interaction and dominance rather than a sexual preference, this may be true for many species but bonobos are the best candidate for similarity. Sexual behaviour is a subject of great psychosocial and medical importance in humans. The bonobo is very sexually active, and forms, therefore, an important study subject in this respect (Wrangham 1993). The prolonged oestrus of female bonobos shows parallels with human females, but this pattern can be seen in many other primates as well and the significance of this prolonged oestrus may vary from species to species (Furuichi 1992:179). For chimpanzee females, benefits of prolonged sexual swellings included more access to food (food exchange for sex), better relations with males including grooming and tolerance. Costs include higher energy levels needed, restriction of posture (sitting); females may attract other groups including rival males. Also reduced feeding opportunities and harassment from males within and outside of the group. For bonobos, females are able to form alliances against males and therefore control food resources,

therefore energy levels are less of a problem and male aggression and tolerance is not a problem (Kano 1992, Parish & de Waal 1992).

Regarding human homosexuality, Kirkpatrick (2000) suggests, “the evolution of human homosexuality is tied to the benefits of same-sex affiliation” (2000:14). Therefore as natural selection supports this same-sex affiliation, both sexes need to form bonds with partners of both sexes (Kirkpatrick 2000:14). Kirkpatrick also proposes that being attracted to same sex individuals and expressing this does not contradict or is not an alternative for opposite sex relations (Kirkpatrick 2000:14). Homosexuality was, and is, widespread across human cultures. In classical Athens men were ‘expected’ to be attracted to other men, usually an older dominant man and a younger submissive male (Kirkpatrick 2000:15) The Sambia of New Guinea ‘instruct’ boys into manhood, all boys participate in homosexual activity before marriage, it is believed to be ‘necessary’ in order for a boy to become a man (Herdt 1984). Although following marriage, this activity ceases, and this does not make them homosexual in orientation, and this is a social practice, rather than sexual preference (Herdt 1984).

Anthropologists Lovejoy (1981) and Fisher (1983) suggest that in humans partial separation between sex and food mutually benefits men and women. A woman can mate throughout her cycle and can exchange sex for male commitment and parental care, cementing the bonds between them. Bonobos appear to fit this model in key points, that females also have extended receptivity and can use sex to gain male favours, for example food (Lovejoy 1981, Fisher 1983).

Bonobos however, show more elaborate sexual behaviour, than most primates in that all maybe in all age/sexual combinations that, moreover, can be displayed in a variety of social contexts. This is specific for bonobos among the non-human primates. It suggests that sexual behaviour serves extensive secondary functions in this species also. To investigate the possibilities of a function other than reproduction, we have to analyse the benefits for an

individual of the behaviour and how the behaviour contrasts to the survival value (Tinbergen 1963).

For the two *Pan* species copulations of around 20 seconds are shorter than those of a gorilla (1-1.5 minutes). Although bonobos have a longer duration on average, usually double the time and five times more thrusts per copulation than a chimpanzee, investing far more energy (Kano 1992:156). Captive-reared chimpanzees tend to have unusually high sexual activity, possibly due to increased time not taken up with activities such as foraging (Kano 1992:157). However, although higher than in the wild, levels of sexual activity never reach the levels found in wild bonobo groups (Kano 1992:157).

1.4 The validity of captive studies to investigating function

The captive groups differ in a number of respects to those found in the wild, firstly group size. Limited group size is a major problem for captive primate groups generally, a small captive population has a limited gene pool, but this also creates problems for behavioural studies. In an ideal situation a species would be kept in natural sized groups and this is especially a challenge in captive bonobos because of the limited number of captive individuals worldwide. Consequently individual captive group sizes are considerably smaller than in the wild. As a result there are limited opportunities for social interaction. Parish (1996) rightly states that there should be caution exercised when analysing data from captive studies, particularly when function or survival value is being analysed. Tinbergen (1963) was the first to suggest four questions that can be asked about a behaviour pattern. Firstly, the proximate mechanism or immediate causes. Secondly the development of the behaviour over an individual's lifespan. Thirdly the function of the behaviour and evolutionary advantages, and the evolutionary history, why a particular trait characterises a species. This includes function of particular behaviours as this study represents. Parish (1994) et al. argue that rates

and types of sexual behaviour in captivity correlate closely with those in the wild (de Waal 1987, 88, 89, Kano 1992). Furthermore, that 'captivity offers a practical opportunity to gather detailed data, for instance on complex inter and intrasexual affiliations, impossible to undertake in the wild (1996:66). The opportunity to study bonobos in a captive situation enables socio-sexual behaviour to be observed at close range, in varying social situations and between known individuals, and this is a main objective of my study. Small captive groups may limit or alternatively magnify the type and frequency of various types of social behaviour as well as the distribution of sexual behaviours across age/sex categories. For example, adult male bonobos in captive groups are often under-represented with more females than males. This could for example lead to possible unrepresentative frequency and distribution of sexual behaviour within and between age/sex categories. Moreover such age/sex distribution may actually affect the nature of the sexual behaviour (de Waal 1987, Kano 1992).

It is evident that some interesting questions about sexual behaviour and dominance relationships among and between the sexes are still unanswered.

1.5 Socio-sexual Behaviour in general

In order to understand socio-sexual behaviour in bonobos, firstly we must consider socio-sexual behaviour in a wider perspective. Wickler (1967), cited in Wrangham (1993), introduced the concept of socio-sexual behaviour, describing non-conceptive sex as having evolved to serve in communication as a secondary function (Wrangham 1993:66). For example male/male mounting behaviour seen in a number of primate species including macaques, baboons and gorillas, which would have a function in the regulation of dominance relationships. In Mandrills (*Mandrillus Sphinx*) high-ranking males will touch a low ranking male's genitals, usually initiated by the low ranking individual (Dixson 1998:146). Another example is Hanuman langurs (*Presbytis entellus*), where out of 524 mounts observed,

dominant adult females (84% of such cases) mounted a lower ranking female (Srivastava et al. 1991). In mountain gorillas (*Gorilla gorilla beringei*) at Virunga, 'homosexual' behaviour, including anal intromission, occurs between different aged pairs (silverback and blackback) in all male groups and Yamagiwa (1987) observed 98 instances of homosexual mountings between males, both dorso-ventrally and ventro-ventrally (Yamagiwa 1987).

Penile erection other than during copulation is also frequently observed in many primates (Dixon 1998:150). In both chimpanzees and bonobos (as well as in many other species) an erect penis is exhibited during the initial stages of heterosexual encounters. Penile erections however, may also occur during play, for instance in the Sumatran orang-utan (*Pongo Pygmaeus abelii*) (Rijksen 1978) and in chimpanzees and bonobos (de Waal 1987, 1990, Hashimoto et al. 1994) or while a male is being groomed (Dixon et al. 1975). It must be noted at this point that, although such behaviour could be labelled as "socio-sexual" this may not necessarily imply a secondary function: general excitement or arousal may result in the erection of the penis. In some species, penile displays are shown in very specific non-sexual contexts. An example of ritualised genital displays occurs in squirrel monkeys (*Saimiri sciureus*) (Ploog 1967). Three types of display posture often occur with penile or clitoral erections and these displays appear to be for communication functions related to dominance (Ploog 1967). In the common marmoset (*Callithrix jacchus*), for example, both sexes display their genital region in agonistic interactions and usually dominant individuals towards subordinates. Common marmosets are also known to exhibit male/male copulation with intromission (Epple 1975). Although it is also possible that this behaviour has not evolved to serve a secondary function, distinct from the original copulatory one, but is a side effect of the behavioural regulatory systems. There is the possibility that the behaviour serves a specific *secondary function*. In this case the behaviour would have to contribute to survival and/or reproduction.

De Waal (1995) points out how different chimpanzees and bonobos are with regard to socio-sexual behaviour. He argues that in chimpanzees, reproduction is the main function of sexual behaviour and that non-reproductive sexual behaviour in this species is limited to presenting and inspection. He suggests that in bonobos, however, socio-sexual behaviours serve a similar function to embracing and kissing in chimpanzees, namely reconciliation (1995:51). To back up his claim, de Waal points out that the presence of food is often associated with the occurrence of socio-sexual behaviour in his captive group, as well as in wild studies and that this points towards a tension reduction function. Thompson-Handler et al (1984) reported sexual behaviour when bonobos arrived at a fruiting tree, or when a prey item was caught, and that it was followed by calm feeding.

Beach (1976) suggests that a greater encephalisation may have allowed a greater liberation from the hormonal regulation of sexual behaviour and hence the evolution of new functions. This would be supported by two species with some of the largest brains; bottlenosed dolphins (*Tursiops truncatus*) (Booth 1989) and bonobos. Wallen (2001) found that in primates, including humans, the independence between hormones and sexual behaviour allows sex to be used in nonreproductive contexts, for social purposes. This separation of the ability to mate from sexual motivation allows social experience together with social context to have an effect on the expression of sexual behavior in nonhuman primates, both during adolescence and in adulthood (Wallen 2001:340).

1.6 Socio-sexual behaviour: functions

Socio-sexual behaviour is proposed to serve the following functions:

- 1) Bonding of pairs and the related protection of young.

This relates to monogamous pairs and therefore is not testable or appropriate for my study.

- 2) Group cohesion, where sex gives both sexes something to remain together for.

For the male, he may sire any offspring produced, for the female as mentioned previously protection of any offspring is vitally important. Also in bonobos such sexual behaviours appear to assist in group cohesion between males and females, and such behaviours are unique to bonobos (Kuroda 1980). This possible function can be studied in captive groups and will form one of my hypotheses.

3) Greater access to food, which also benefits the long-term viability of any offspring. Food ownership will be studied in relation to my conflict reduction hypothesis.

What makes the bonobo different from other species, including other non-human primates, is the extent and complexity to which sexual behaviours have permeated social life (Manson et al 1997, de Waal 1997). Bonobo sexual behaviour involving 'non-fertile' (same sex, adult/juvenile) pairs is common, occurring regularly in many different social interactions. Examples include feeding situations, reconciliation after social conflicts and in relaxed social situations like play (de Waal 1997). For this study I will systematically analyse the different potential advantages of the non-reproductive sexual behaviour and attempt to decide what possible biological social functions it may have.

Wrangham (1993) cited in de Waal (1990), suggests that chimpanzee and bonobo sexual behaviour can be classified functionally in five categories; 1) conception, 2) practice, 3) paternity confusion (Hrdy 1981), 4) exchange and 5) communication. Wrangham argues that a sexual interaction may cover more than one category. He suggests that it is this latter category; "communication sex" that is only applicable to bonobos (1993:58), but as discussed below, communication sex is found in other species. These function categories will now be discussed in more detail.

1) With regard to conception chimpanzee males recognise when females reach maximal tumescence as intense aggression/conflict and copulation occur, for bonobos there is no evidence that males recognise probable ovulation time, with increased mating and

aggression, suggesting ovulation is concealed. If this is true then it explains low aggression between bonobo males (Wrangham 1993:60).

2) The paternity confusion hypothesis is the most applicable mating system hypothesis for chimpanzees and bonobos, as it concentrates on differences between single male and multi male groups, all with several females. In single male groups like gorillas sex is usually for reproduction only. Multi male groups including chimpanzees and bonobos usually have a high rate of non-conceptive sex. This is suggested to partially conceal ovulation and give long periods of receptivity (Hrdy 1981). Evidence from macaques and baboons suggest that the proximate goal of female choice is mating with various males instead of one particular individual (de Ruiter et al. 1994; Bercovitch 1995) supporting the hypothesis that promiscuous mating by females is to produce paternity confusion (Hrdy 1987). With the paternity confusion hypothesis the male's possible perceived certainty of being the father of an infant is altered by female sexuality. Males will be unable to discriminate which infants will be his as he has mated with many females and males will therefore support mothers and protect infants (Andelman 1987, Hrdy 1987). Chimpanzees and bonobos fit the paternity confusion hypothesis well (Wrangham 1993:51). Wrangham suggested that the universality of paternity-confusion sex gave rise to the evolution of exchange sex in *Pan* and of communication sex in *P. Paniscus*' (Manson et al 1997:780). However, Wrangham does not explain how communication sex, which developed from the paternity-confusion hypothesis, relates to the genito-genital rubbing (GG rubbing) behaviour in female bonobos. For paternity confusion in chimpanzees the female is maximally swollen for more days when she is infertile than when she is fertile. While infertile she mates with many males, especially immature ones (Goodall 1986; Hasegawa and Hiraiwa-Hasegawa 1983). Female chimpanzees also have many periods of swelling while infertile, for example during adolescence and pregnancy and copulations occur in all these cycles (Goodall 1986). The time a female is actually fertile is

12% of all cycles and for bonobo females, with longer periods of swelling and more frequent swellings, especially while carrying an infant, this figure is far fewer, around 2% (Wrangham 1993:61).

3) An alternative hypothesis is practice. This is infertile copulations by immature females or males and this involves improving the sexual technique, for females this is especially so during adolescence when still unable to conceive. Males begin while infant, although the same can be said of bonobo females. Copulation rates are most frequent among young males and decline with age. Hausfater (1975) suggests social learning is important, in which contexts it is 'appropriate' to initiate sex. Although it is doubtful though, that this high rate of immature sex is due to practice, and for chimpanzees and bonobos the rate is far higher than other primates with similar sexual patterns, for example, baboons (*Papio cynocephalus*) Hausfater (1975).

4) Another hypothesis is the exchange of sex for food or other social benefits, for example, alliance formation. Exchange applies when a female receives non-reproductive benefits like food, while a male mates with a female, and the male believes she is fertile. A female with a sexual swelling is more successful in obtaining food (de Waal 1990, Goodall 1986 Kuroda 1984). For bonobos sexual behaviour itself is the 'aim' with subordinate individuals more successful in obtaining food immediately after a sexual contact than without sexual behaviour (de Waal 1987, Wrangham 1993).

5) Communication sex is defined as "sexual interactions in which neither partner obtains conceptive benefits" (Wrangham 1993:64). This is a somewhat vague description and. De Waal suggests two further criteria:

- 1) that sexual contact is not a replacement for heterosexual sex, where males without females engage in same-sex sexual activity
- 2) that the sexual behaviour should be an integral part of 'normal' social life (1990, 1992).

Such sexual contact may or may not include intercourse, and only bonobos have evidence for communication sex (Kano 1992, Kitamura 1989, Kuroda 1984). An example of such behaviour is GG rubbing by adult female bonobos, used extensively in many social contexts and in the presence of males. As for the possible functions of communication sex one possible explanation is from Smuts and Watanabe (1990), who propose, 'the offering of one's genitals to another may gain its meaning partly by its honest communication of vulnerability, in other words, by reliably risking enough to make one's interest in the relationship likely to be genuine'. De Waal (1990, 1992) supports this view, stating 'communication sex is sexual interactions in which neither partner obtains conceptive benefits'. This suggests further components, that communication sex should occur not as a substitute for heterosexual sexual behaviour due to lack of opposite sex partners for example and that sexual behaviour is part of a species' social behaviour i.e. socio-sexual behaviour. Communication sex maybe also for the 'benefit' of third parties, for two bonobo females to engage in sexual behaviour may show a male that a close bond or alliance has been formed and thus prevent male aggression. Other species to exhibit communication sex include bottle-nosed dolphins (Wrangham 1993:68, Booth 1989).

Hashimoto et al. (1994) studied bonobo behaviour in the wild and they concluded that the most important function of non-reproductive sexual behaviour is tension reduction, both within and between groups. Such sexual behaviour appears to assist in allowing individuals to co-exist peacefully as it often occurs following agonistic interactions or intense excitement (1994:165). For example, several groups meeting at a food source, where rather than aggression and the potential risks to all involved, a subordinate individual may initiate sex with a more dominant individual and each may then feed relatively peaceably. The sexual behaviour between adults and juveniles is proposed as essential in social cohesion of the bonobo group. De Waal also supports this view, suggesting social bonding is why sexual

behaviour occurs so frequently, and across all sex/age combinations. As females are at the core of bonobo society, bonding appears to support why genito-genital (GG) rubbing is so frequent between bonobo females; being a method of tension regulation, where female conflict would be detrimental to the group as a whole (Hashimoto et al. 1994). This GG rubbing behaviour is unique to adult female bonobos and is primarily characterised by a ventro-ventral or 'face to face' position. This position is also a frequent copulation position between males and females, as documented evidence from both wild and captive studies has shown (Hashimoto et al. 1994, Kano 1992, de Waal 1987). Kuroda's (1980) study found that GG rubbing was only observed in large groups, especially when the whole group was excited (1980:190). The position of the female bonobos vulva, being frontally located, allows easier intromission during copulation ventro-ventrally. Subordinate females, in both captive and wild groups, most often initiate such GG rubbing, which supports the view of reducing tension (Kano 1989, Hohmann et al 2000). Between male bonobos also, though less frequently than between females, non-copulatory socio-sexual behaviour, like genital massage and oral sex, are utilised to reduce tension or aggression instead of the various social behaviours seen between chimpanzee males like the pant grunt (Hashimoto et al. 1994). Similar results regarding dominance and initiation were found in a study of talapoin monkeys (*Miopithecus talapoin*) where in a captive group, 80% of same sex socio-sexual presentations were made by low-ranking individuals towards high-ranking individuals. Also 87% of all mounts were by high-ranking individuals on low ranking individuals they had recently agonised (Dixson et al 1975:178/9).

1.7 Socio-sexual behaviour: description

Socio-sexual behaviour is particularly evident during group social interaction, especially where food is concerned, whether provisioned or natural food items (Kuroda 1980). Kano (1989) described four main types of genital contacts not involving copulation; these are: 1) GG rubbing, 2) mounting, 3) rump contact and 4) penis fencing. De Waal (1995) on the other hand described six types of 'socio-sexual' behaviour from studying a group of captive bonobos at San Diego Zoo. These are: 1) ventro-ventral, 2) ventro-dorsal, 3) opposite, 4) genital massage, 5) oral sex and 6) mouth kiss and these are the categories I have used in my study (see page 38 for description). Although captive studies are often seen as limited in what researchers can ascertain, there is one important factor that cannot often be viewed in the wild and that is detail.

This study will focus on describing hypotheses regarding the context and possible function of socio-sexual behaviour by members of a group of captive bonobos from Twycross Zoo, with additional data from another bonobo group in Planckendael Zoological Park, Belgium. The Planckendael group has a similar composition (4 males and 4 females) to that of Twycross, and data from both groups will be compared to other captive and wild studies. To enable me to formulate hypotheses that can be tested on the Twycross group, I collated data on socio-sexual behaviours from a range of articles for each age/sex category illustrated in the matrix below. This allows a clear visual representation of what socio-sexual behaviours have been recorded for each age/sex category, and more importantly any categories where data is absent or lacking.

Socio-sexual behaviours according to Age/Sex category

	Adult (M)	Adult (F)	Adel (M)	Adol (F)	Juv (M)	Juv (F)	Inf (M)	Inf (F)
<u>Adult Male</u>	DV-2 RR-2	DV-1,2 VV-1, 3,5 RR-2	DV-2, 3 RR-2 VV-2, 3 GM-3 MK-3 OP-3	DV-2 VV-5	DV- 2* , 4 VV- 2* , 4 RR-2	DV- 2* , 4,6* VV- 2* , 4 GM-5	VV-6	VV- 3
<u>Adult Female</u>	DV- 3 GM- 3 VV- 3	GG-1, 2 VV- 3 , 5 OP- 3 GM-5 MK- 3 , 5	DV-2, 3 VV-2, 3 MK- 3	DV-2 VV-2, 5 GM-5	DV-2, 4 VV-2, 4 RR-4	VV-2, 4,5 GM-5 OS-5 MK-5	VV-6	VV- 3
<u>Adol Male</u>		VV- 3 DV- 3 GM- 3	VV- 3		DV-2, 4 VV-2, 4	DV-2 VV-2		VV- 3 VD- 3
<u>Adol Female</u>					DV-2 VV-2	VV-2, 5 GM-5 MK-5		
<u>Juv Male</u>					DV-2, 3 VV-3, 4 GM- 3 OS- 3 MK- 3	DV-4, 6* VV-2, 3,6* MK- 3 OS- 3		VV-6
<u>Juv Female</u>					MK- 3 VV- 3 , 6* OS- 3 GM- 3	MK- 3		
<u>Inf (male)</u>		VD- 6* VV- 6*						
<u>Inf (Female)</u>	VV- 3 VD- 3	VV- 3 VD- 3	VV- 3 VD- 3 OP-3 MK-3					
<u>Key</u>				<u>References</u>				
DV - dorso-ventral mounting				1: Hohman & Fruth (2000)				
VV - ventro-ventral mounting (includes GG rubbing)				2: Kano (1992) * - initiator/partner known (Blue)				
GM - genital massage MK - mouth kiss				3: De Waal (1989) -all initiator/partner known (Blue)				
OS - oral sex OP – Opposite				4: Hashimoto et al (1994)				
RR - rump-rump contact				5: Manson et al (1997)				
				6: Hashimoto (1997)* - initiator/partner known (Blue)				

For those references where the initiator is known, this is shown on the matrix as the individual in the left (vertical) column, with the partner being the individual on the top (horizontal) of the matrix.
For a more detailed description see the methodology section of this proposal.

Table 1.a. Socio-sexual behaviours according to age/sex category

Table (1.a) illustrates the range of socio-sexual behaviours that have been recorded for bonobos in the various age/sex categories. This matrix only shows the possible *range* of recorded behaviours for each age/sex category and not the frequency of occurrence.

The main references, which have the greatest number of types of behaviours for all age/sex categories, are understandably from captive studies where visibility and greater detail allow this and both de Waal (1989) and Manson et al (1997) are examples of such studies. Kano (1992) on the other hand has also provided a great amount of sexual behaviours on wild groups and is the only reference reviewed based on a wild study listed to do so.

Most captive studies, de Waal (1989) and Manson et al (1997) included, have only one adult male in a group and this is reflected in the matrix where the only sexual interaction between adult males comes from Kano's study (a wild group). Although such research has shown adult male/adult male contact occurs less often than for many other age/sex groups. Adult females on the other hand exhibit a wide range of sexual behaviours and with all age/sex categories. This is to be expected as females are dominant in bonobo society and as such would be expected to be the favoured partner for sexual interactions. Also in captive groups until recently single individuals of each age/sex category predominated, therefore sexual interactions between for example juvenile males were not possible. In the wild where group size is not limited, such behaviours can be observed, yet the difficulty in observational studies limits the number of such incidents being recorded.

De Waal's (1989) study at the San Diego Zoo consisted of ten individual bonobos in three separate groups, although two of these groups were merged shortly before the study ended. This was the largest captive group at the time, although being separated this creates biases in the results on the matrix (reference 3). Sexual behaviour between adults and immature females (juveniles and adolescents) was particularly lacking, the only immature individual in a group with adults being one infant female. This female infant initiates and is

initiated by all the members in that group (adult male, adult female and adolescent male) and this provides valuable information, lacking in the other studies listed (de Waal 1989). An adolescent male was in two of the three groups so adult/adolescent male interactions are recorded. No adolescent females were in any of the groups and juveniles were kept in a group on their own, so no adult/juvenile female sexual behaviour was available. This is unfortunate as it is especially immature sexual behaviour that is often overlooked in wild studies, except Kano (1992) and Hashimoto (1997), captive situations provide the opportunity to investigate this further. Hashimoto (1997) describes the development of socio-sexual behaviour in bonobos, one of the first researchers to do so. Hashimoto observed such behaviour in the wild and classified three categories of behaviour. Firstly play-like genital contact, where immature individuals perform sexual contacts in relaxed social situations whereas for adults socio-sexual behaviour is more likely around tense social situations such as feeding and agonistic interactions. Secondly copulation-like genital contact, immature female/mature male sexual contact occurs to reduce tension. Contact between these individuals will be limited due to the mature males peripheral position in the group. Immature male/mature female sexual contact is frequent possibly because these males can penetrate such mature females, but also because of close association with their mothers' frequent associates. Thirdly genital contact in social contexts, mature females did not GG rub with immature females (1997:2). Hashimoto describes 'Play-like genital contact' and 'copulation-like genital contact', which occur at a very young age. These behaviours have common features with other great apes, rather than being unique to bonobos, although the definitions of 'play-like' and 'copulation-like' are somewhat vague. Although genital contact occurring around play behaviour is much more frequent in bonobos (Hashimoto 1997:18).

One of the main findings was that between mature individuals some form of courtship behaviour occurred prior to sexual contact, whereas such behaviour involving immature

individuals did not (Hashimoto 1997:12). Hashimoto also found that immature males were more sexually active than immature females, immature male/immature male dyads were the most frequent, followed by immature male/immature female dyads and the least frequent being immature female/ immature female dyads (1997:7). Genital contacts also occurred more frequently between siblings than between non-siblings. Sexual contact between immature males and mature females was very frequent and this increased with the male's age. Immature females on the other hand had no sexual contact with mature females, although in a captive group de Waal found this did occur but between mother and offspring (de Waal 1989, Hashimoto 1997:9).

The frequency and range of socio-sexual behaviours across the age/sex groups is particularly lacking in information. Any frequencies that have been published are mainly focused on copulation frequencies between males and females. The exception again is de Waal, who as well as providing information on initiation, also provides frequencies for the six socio-sexual behaviours he devised, taken over almost 300 hours of observations, which is shown below (de Waal 1989).

	Ventro- Ventral	Dorso -Ventral	Opposite	Genital Massage	Oral Sex	Mouth Kiss	Total
Total	420	156	23	39	17	43	698

Table 1.b Frequency of socio-sexual behaviour – San Diego (de Waal 1989)

This table illustrates that for the San Diego groups ventro-ventral mounting was by far the most frequent socio-sexual behaviour, whereas in wild studies dorso-ventral mountings predominated (Kano 1992).

I will now proceed to describe theories centred on my hypotheses, theories on reconciliation, tension reduction, social status (dominance) and social bonding. I will subsequently discuss grooming behaviour, in relation to my social bonding hypothesis.

1.8 Reconciliation and tension reduction.

Reconciliation is that primates can remember which individuals they had conflict with and show 'selective attraction' to this individual following a dispute, followed by amicable contact that can bring their friendship back to the pre-conflict level (Cords & Aurelli 1996). De Waal and van Roosmalen (1979) were the first to find evidence for this in chimpanzees, although de Waal and Yoshihara (1983) later conducted more controlled observations on macaques (*Macaca mulatta*) (de Waal 1983, 1987:320). Reconciliation where former opponents are attracted following a dispute has been documented in about 20 species of primate, yet the focus has mainly concerned the occurrence and type of reconciliation and not the function of reconciliation (Cords et al. 1996:42).

Reconciliation following agonistic interactions has also been observed in other species, for example bottlenosed dolphins (*tursiops truncatus*) and spotted hyenas (*Crocota crocuta*). Both of these species, like the two *Pan* species, are group living social animals that live in fission/fusion societies (Connor et al 1998 and Hofer et al 1993).

De Waal suggests that for bonobos only studies on captive bonobos can deduce whether socio-sexual behaviour is caused by food or tense social situations. De Waal states that 'the behaviour for re-establishing contact can be assumed to be similar to that in the natural condition'. Goodall (1986) supports this in chimpanzees, confirming that reconciliation in chimpanzees of Gombe National Park, Tanzania, is very similar to that of captive chimpanzees at Arnhem Zoo (de Waal 1982, de Waal and van Roosmalen 1979, de Waal 1997:321).

Regarding the relationship between food and sex, at a simple level it creates excitement, which then "sparks over" into sexual arousal or as De Waal calls it, the "arousal-transformation" hypothesis. Alternatively Kano (1980) and Kuroda (1984) suggest that socio-

sexual behaviour occurs when a potential for aggression occurs, which is what de Waal calls the “tension-regulation” hypothesis. The main difference is that only the tension regulation hypothesis supposes that sexual behaviour occurs in tense social situations unrelated to food (de Waal 1987:320).

De Waal suggests that socio-sexual behaviour as a tension reducing mechanism evolved from the original function of sex, the male/female relationship, and that it evolved to cover all age/sex combinations. This is supported by wild studies where bonobo male/female relationships are more relaxed and less tense than chimpanzees (de Waal 1995:53).

1.9 Social Status and Social Bonding

Furuichi (1997) studied dominance interactions in wild and found these were determined by agonistic interactions and were found to be very frequent between males and less so between females or males and females (1997:859). Furuichi found that male bonobo agonism occurred mainly in three situations: 1) when males became excited on finding food or hearing another group vocalise, 2) ‘play-like agonism’ where interactions are low in aggression and more ritualised, often older adolescent males and 3) to dominate another individual and display openly, which is not frequent overall but more so in late adolescence (1997:862). Female agonism was much less frequent and followed a more linear hierarchy than for males, according to age. Agonism occurred mainly between high-ranking females and mainly during feeding situations, although not directed at food competition (1997:863).

1.10 Grooming

Allogrooming interactions will be analysed in conjunction with socio-sexual behaviour in hypothesis 4 prediction 2, and therefore I have included a brief description of allogrooming in bonobos. Allogrooming is widespread throughout the animal kingdom and

serves many social functions, increasing group cohesion (Borries et al. 1994, Cheney 1992), cement social bonds, reduce tension and is dominance related (Nishida 1979, Goodall 1986, de Waal 1982). In the wild bonobos spend on average 5.7% of daytime activity allogrooming, which is their most frequent social activity (White 1996). For captive bonobos this is much higher around 13%. This lower frequency for wild bonobos may be related to the time spent feeding, which accounts for 40% of the daytime activity (White 1996), whereas captive groups spend less than 20% of the day feeding (Franz 1999:539). In bonobos allogrooming is most frequent between male/female dyads and less so between male/male dyads. Female/female allogrooming is frequent, unlike in Chimpanzees. (Kuroda 1979, Kano 1980, 1992, Badrian et al 1984, Furuichi 1989, Idani 1991, Ihobe 1992, Furuichi & Ihobe 1994). Old females are high status, often dominating males (Kano 1992, Ihobe 1992, Parish 1996). The dominance of males is strongly correlated with the presence or absence of their mother, supporting sons in disputes (Furuichi 1989, 1997, Ihobe 1992, Kano 1992, Furuichi & Ihobe 1994). It was found that adult females received more allogrooming than any other age/sex class, but between females there is no significant difference between dominant and subordinate grooming. Given this the most frequent grooming was between adult males and adult females, the same as in the wild (Kano 1980, 1992, Badrian et al. 1984, Idani 1991). Most male/female grooming in the wild, however occurred between mother-son pairs and allogrooming between unrelated males and females is more infrequent (Furuichi 1989, 1997, Ihobe 1992, Kano 1992, Furuichi & Ihobe 1994).

All the hypotheses below were taken from Hohmann & Fruth (2000), apart from some additional predictions added by myself. This paper, as well as being very recent, also concentrated on genito-genital (GG) contacts (ventro-ventral mounting between females). Although in Hohmann & Fruth's paper only adult females and ventro-ventral mounting was studied, the hypotheses were thought to be testable for all age/sex groups and types of socio-sexual behaviour, especially in a captive situation.

On the basis of the literature cited previously (Kano, de Waal, Hohmann & Fruth, Hashimoto and others) hypotheses from these sources have been used together with additional predictions, which can be tested in my captive groups.

Hypothesis I: Reconciliation is in the form of socio-sexual behaviours.

Bonobos, like other primates, exchange affiliative or friendly behaviours between individuals after an agonistic or aggressive encounter. Additionally reconciliation is related to close social ties and or kinship and this is reflected in the predictions.

Hypothesis II: Socio-sexual behaviours are a form of tension reduction.

A major function of socio-sexual behaviour, proposed by Hanby (1977) in non-human primates is to reduce tension. De Waal (1987) suggests that captive primates in a reduced living space have lower rates of aggression but higher rates of social tension.

Hypothesis III: Socio-sexual behaviours are an expression of social status.

The relationship between any two individuals reflects their social status and usually one is more dominant and the other more submissive. In bonobos such social status behaviours may take the form of socio-sexual behaviours.

Hypothesis IV: Social bonding is increased by the occurrence of frequent genital contacts

Many researchers including Kano (1980) and Kuroda (1984) suggest that socio-sexual behaviours are affiliative and as such it is to be expected that individuals who associate frequently also have frequent socio-sexual contact.

Hypothesis 1: Reconciliation is in the form of socio-sexual behaviours

Prediction 1: Socio-sexual behaviour follows agonistic interactions

For this prediction socio-sexual behaviour between all age/sex groups will be observed using all occurrences sampling and data collated in relation to whether such behaviour followed agonistic interactions. Agonistic interactions will also be recorded using all occurrences sampling and socio-sexual behaviour that occurs within a cut off point of 10 minutes after the agonism occurred. All occurrences sampling will be used.

Prediction 2: Rates of socio-sexual behaviours increase after agonism

A comparison of pre-conflict and post-conflict rates of socio-sexual behaviours will be used to test this prediction. The expectation being that such behaviours occur more frequently following rather than before agonistic interactions.

All socio-sexual behaviour shortly before and following agonistic interactions will be recorded by all occurrences sampling within a cut off point of 10 minutes before and after an agonistic interaction.

Prediction 3: Individuals frequently in close proximity sexually reconcile more than individuals who are not frequently in close proximity.

Data for proximity will be obtained using nearest neighbour analysis. Using Scan sampling at regular intervals during the day (every 30 minutes) all individuals will be

observed, noting which individual is nearest to which individual. The data will be analysed as to whether individuals most frequently in close proximity reconcile more frequently and vice versa.

Hypothesis 2: Socio-sexual behaviours are a form of tension reduction

Prediction 1: In feeding situations socio-sexual behaviours occur more often between owners of food and bystanders than between bystanders.

During feeding the frequency of socio-sexual contact between individuals who possess food and individuals who do not, and between individuals who do not possess food will be observed. The data will be recorded using all occurrences sampling throughout feeding sessions.

Prediction 2: The average duration of socio-sexual contacts would be expected to be higher during feeding, where tension is high, than in a non-feeding context.

For this prediction data on individuals engaged in socio-sexual behaviour prior to and during feeding situations will be compared to non-feeding times (a comparable number of occurrences over certain time period, the same time of day if possible). All occurrences sampling will be used to record the observations.

Prediction 3: Socio-sexual behaviour will be frequent between different age categories to reduce tension

Individuals will be group together into age categories (juvenile, adolescent, young adult, adult) and the frequency of socio-sexual behaviour between these groups will be recorded using all occurrences sampling.

Prediction 4: Initiation of socio-sexual behaviour will be frequent between same sex individuals (non-fertile pairs)

The frequency of same sex dyad socio-sexual behaviour compared to mixed sex dyad socio-sexual behaviour recorded using occurrences sampling

Prediction 5: Assuming dominance plays a role in tension regulation, dorso-ventral and ventro-ventral mounting would be expected to be more frequent than non-mounting socio-sexual behaviour

All socio-sexual behaviours will be observed using all occurrences sampling of mounting (dorso-ventral and ventro-ventral) versus non-mounting socio-sexual behaviours to enable further analysis.

Hypothesis 3: Socio-sexual behaviours are an expression of social status

Prediction 1: Initiation of socio-sexual behaviour shows status-dependent asymmetries

The social status or rank of each individual will be determined using agonistic interactions and displacement data. Using all occurrences sampling observations on which individuals initiate socio-sexual contact and which receive it will be recorded. Subordinate females are reported to initiate socio-sexual contact with a ventral presentation.

Prediction 2: Individual spatial position shows status-dependent asymmetries, whether the individual is in the top or bottom position – horizontal only.

For this prediction only socio-sexual behaviour that involves mounting where individuals are in a top/bottom position will be recorded using all occurrences sampling (ventro-ventral or dorso-ventral socio-sexual behaviour). The data will be analysed in relation to the rank status in the group.

Prediction 3: High status/low status dyads have socio-sexual contact more frequently and for a longer duration than high status/high status or low status/low status dyads

Socio-sexual behaviour frequencies and rank status of all individuals will be analysed following data collection via all occurrences sampling and focal behaviour sampling.

Hypothesis 4: The function of socio-sexual behaviour is social bonding

Prediction 1: High frequency of socio-sexual behaviour between close spatial associates

Individuals frequently in close proximity to one another will have a high frequency of socio-sexual contact. Proximity data will be collected by nearest neighbour analysis, using scan sampling to ascertain individuals most often in close proximity to one another and whether such individuals display frequent socio-sexual contact.

Prediction 2: Individuals who are frequent socio-sexual partners will also be frequent grooming partners

Data on grooming frequencies and socio-sexual behaviour frequencies between all individuals will be collected using all occurrences sampling.

Prediction 3: High frequency of socio-sexual contact between individuals of differing rank

Socio-sexual behaviour frequencies and rank status of all individuals will be analysed following data collection via all occurrences sampling and focal behaviour sampling.

2.0

Methodology

2.1 Study Subjects: Twycross

The study group at Twycross Zoo is the only group of captive bonobos in the United Kingdom. The first individuals came from European Zoos in 1992, namely Diatou, the current dominant female and her then dependent daughter Kichele. Another individual, Kuni, arrived at the same time, but was moved to another zoo shortly after (Marcus Smith pers. comm.). Kakowet II, the dominant male, arrived soon after, from San Diego Zoo to start the foundations of a new breeding group. The first UK born bonobo, Ke Ke, a male, was born in 1994, followed by Yasa, a female in 1997. Banya and Jasongo are the most recent additions to the group. Banya, a young female, came from Cologne Zoo and Jasongo, a young male, from Wuppertal Zoo. Towards the end of the study Banya gave birth to her first infant, a female Kya, who was rejected and later hand reared. The following table illustrates the key features for each individual.

There are seven individuals at Twycross and these are as follows:

Name	Sex	DOB/Age	Place of Birth	Characteristics
<i>Diatou</i>	Female	1977-25 years	Stuttgart Zoo	Dominant, oldest and largest female
<i>Kichele</i>	Female	1989-13 years	Stuttgart Zoo	Daughter of <i>Diatou</i> ,
<i>Banya</i>	Female	1990-12 years	Cologne Zoo	Unrelated female, smallest adult female
<i>Yasa</i>	Female	1997- 5 years	Twycross Zoo	Daughter of <i>Diatou</i> & <i>Kakowet II</i>
<i>Kakowet II</i>	Male	1980-22 years	San Diego Zoo	Dominant male
<i>Ke Ke</i>	Male	1994- 8 years	Twycross Zoo	Son of <i>Diatou</i> & <i>Kakowet II</i>
<i>Jasongo</i>	Male	1990-12 years	Wuppertal Zoo	Unrelated male*, most subordinate

Table 2.a Description of individuals in Twycross group

Therefore, regarding the age/sex categories listed on page 39, the Twycross group consists of two adult males (one older and one younger), three adult females (one older and

two younger), one adolescent male and one juvenile female. For this reason, another two age/sex categories have been include, Young Adult Males and Young Adult Females. These will include Kichele, Banya and Jasongo as it was felt that these three individuals differed greatly from the mature adults, Diatou and Kakowet II. Unusually for a bonobo group, Kichele, the eldest daughter of the dominant female has remained with the group, although she is unrelated to the dominant male. Also the youngest adult male, Jasongo would in the wild have remained in his natal group.

*Interestingly I later discovered that Jasongo is related to the dominant female Diatou and her offspring, Jasongo's mother and Diatou are full sisters (Bonobo studbook 2000).

2.2 Factors affecting the results – Twycross

The following factors I feel are important in interpreting the results and overall pattern of socio-sexual behaviours within the Twycross group.

Jasongo, the most subordinate individual was absent from the group on eight out of twenty seven days, almost 30% of the time. He was the constant target of agonism in most instances and some days he 'did not want to leave the sleeping area', preferring time on his own (pers comm.). He did integrate well with the group, playing and grooming, it was only in times of tense social situations that he became really agitated. Banya on the other hand was always an outsider, I never observed her to play and she infrequently initiated any kind of contact with other group members although was frequently a receiver of interactions.

2.3 Study subjects: Planckendael

The second bonobo group that I studied in Planckendael Zoological Park, Belgium, are similar in age/sex combination and group size.

Name	Sex	DOB/Age	Place of Birth	Characteristics
<i>Dzeeta</i>	Female	1971	Wild – Congo	Oldest female, very large swelling
<i>Hermien</i>	Female	1978	Wild – Congo	Mother of <i>Zomi</i>
<i>Hortense</i>	Female	1978	Wild – Congo	Mother of <i>Zamba</i>
<i>Redy</i>	Male	24/11/90	Planckendael	Dominant male, son of <i>Hortense</i>
<i>Kidogo</i>	Male	28/02/83	Stuttgart	Oldest male, smaller than <i>Redy</i> , most subordinate
<i>Vifijio</i>	Male	23/07/94	Planckendael	Adolescent male, son of <i>Hortense</i>
<i>Zamba</i>	Male	16/04/98	Planckendael	Juvenile male, son of <i>Hortense</i>
<i>Zomi</i>	Female	29/01/98	Planckendael	Juvenile female, daughter of <i>Hermien</i>

Table 2.b Description of individuals in Planckendael group

Background information was limited on these individuals other than that provided in the table above. The group consisted of two adult males (Kidogo and Redy), three adult females (Dzeeta, Hortense and Hermien), an adolescent male (Vifijio) and two juveniles (Zomi and Zamba). The Planckendael group is housed in an indoor enclosure (300m³) with access to a large outdoor island (3000 square metres).

2.4 Factors affecting the results - Planckendael

With this group, I had a limited period of study time (6 days) and consequently this is reflected in the amount of data. Rank was therefore found to be impossible to ascertain, few displacements and even fewer agonistic interactions were observed, and the following circumstances increased the difficulty. Dzeeta, the oldest female, was the dominant female in Vervaecke et al. (2000:1469) and may still be, but having suffered a stroke approximately 2

years ago, she was very subdued and interacted little with the rest of the group (pers comm.). The group was also 'unsettled' as the dominant male, Desmond, died two years ago resulting in some disputes for dominance between Kidogo the older male and Redy, who is Desmond's son. Although only 11 at the time of observation, Redy was already much larger than Kidogo and very clearly then dominant with Kidogo avoiding any contact with Redy (pers comm.). Another factor is that just prior to my visit, two females an adult, Kosana and an adolescent Unga (Hermien's daughter) had been transferred to zoos in America and this probably affected the group further.

2.5 Sampling Methods and Ethogram

In the study I analysed the pattern of occurrence of socio-sexual behaviours and the distribution across different individuals and in different contexts. I followed Altmann (1974) in the approach to observing behaviour, and scan sampling and all occurrence sampling were the main sampling methods used. I recorded a total of 146 hours for the Twycross group and 37 ½ hours for the Planckendael group. An ethogram is a list and the descriptions of the species-typical behaviours that are associated with a species and the behaviours used are listed on Pg. 38 (Lehner 1987).

All socio-sexual behaviours were recorded using a combination of check sheets, together with video recording and additional notes. The video camera was especially useful for intense activities involving the whole group, such as feeding and socio-sexual behaviours and agonistic interactions. For proximity data (nearest neighbour analysis) this was collected using scan sampling at half hourly intervals throughout the observation period. Scan sampling means that the whole group is rapidly scanned at regular intervals and the behaviour of each individual is recorded (Martin et al 1993:85). This provides data for all the group members at a given time and is especially suitable for small groups and has been used by Altmann (1970)

and Chalmers (1968) on baboons (*Papio anubis*) and grey-cheeked mangabeys (*Cercocebus albigena*) (Altman 1974, Chalmers 1968). Scans for each individual cannot occur simultaneously and therefore I gave myself 1 minute as a cut off point to record the data for all individuals, using a stopwatch for accuracy. This method of sampling enables the frequency that an individual is observed exhibiting a particular behaviour at a given point in time and is therefore a good indication of the percentage of time that individual spends in that behaviour, in this case the proximity to particular individuals (Altmann 1974:260).

Agonistic interactions were also recorded using all occurrences sampling, each occurrence of a particular behaviour is recorded together with the time (Martin et al 1993:88). These observations enabled data to be collected to enable the various hypotheses to be tested, with regard to the function of these behaviours as previously outlined. The materials used were a Canon U100 video camera, clipboard and check sheets, note pad, stopwatch and pencils/pens.

I used the six socio-sexual behaviour categories defined by De Waal (1989):

- Ventro-ventral mounting: 'face to face' mounting, involving pelvic thrusts, includes genito-genital or GG rubbing of adult females and occurs between all age/sex categories.
- Dorso-ventral mounting: mounting from behind with the mounted individual on all fours. Described as occurring mainly between males and adult females.
- Genital massage: manual stimulation of genital in a rhythmic fashion, both by another individual and self, evidence suggests this is largely a male activity.
- Oral Sex: taking of the penis or clitoris into the mouth. (I found only references for oral sex performed on males, but having observed this on several occasions on a young female, I included both sexes).

- Opposite: where one individual lies on its back and another stands over facing in the opposite direction, while rubbing genitals.
- Mouth kiss: largely restricted to juveniles, one individual places his/her opened mouth over that of another. This category was included as this behaviour occurs in a “sensual way”, unlike that of chimpanzees.

This inventory covers all the main behaviours used in this research and is the most detailed regarding socio-sexual behaviour that I found.

The remaining behaviours involved in testing the following hypotheses are:

- Agonistic interaction: involving an ‘aggressor’ and ‘target’ where one individual, the aggressor, runs to chase another individual, the target. Always involving a full charge, which may or may not involve physical contact.
- Displacement: An individual approaches another individual, who retreats, and this individual may claim the place where the displaced individual moved away from.
- Grooming: Allogrooming, where an individual systematically parts the fur of another individual and maintains the fur and skin.

The age/sex categories varied slightly from researcher to researcher, and I have used the following classifications, which includes an extra category for young adults because of the large age range within the adults at Twycross, from 11 years to 24 years and two distinct age blocks.

- Infant- 0 – 2 years
- Juvenile- 3 – 6 years
- Adolescent- 7 – 10 years
- Young Adult- 11+ years
- Adult-16+years.

First I will present an overview of the socio-sexual behaviours and related behaviour such as agonistic behaviour and proximity. This was included for both the captive groups studied, including type and frequency for each socio-sexual behaviour for all individuals. I also added a section on socio-sexual behaviour in a food context. Following this, data relevant to the various hypotheses will be presented under the headings of each hypothesis and predictions.

The majority of the observations were conducted on the Twycross group and this forms the largest part of the results, followed by additional data collected from a visit to Planckendael in Belgium.

Socio-sexual behaviour and other social behaviour

3.1 Socio-sexual behaviour for the Twycross Group

The total range and frequency of socio-sexual behaviours between the Twycross group is illustrated below in table (3a). As can be seen the most frequent socio-sexual behaviour was dorso-ventral (198 occurrences), closely followed by ventro-ventral (154 occurrences). This was expected and follows patterns observed in the wild and other captive groups (Hohman & Fruth 2000, Hashimoto et al 1994, Kano 1992, 1982, Manson et al 1997, Hashimoto 1997).

Of the remaining socio-sexual behaviours, self-genital massage (118 occurrences) and opposite (90 occurrences) were also relatively frequent, the remaining types much less so. Self-genital massage is not included in table 3a, as this does not occur in a dyad and is described in a separate paragraph on page 45, together with table 3.c for Twycross and table

3.d for Planckendael. Mouth kiss and oral sex were only observed on one occasion, both involving the juvenile female Yasa.

Type and frequency of socio-sexual behaviours for each dyad: Tywcross Group

Dyads	Types of Socio-Sexual Behaviour								Total
	Dorso-ventral	Ventro-ventral	Genital Massage	Oral	Genital Inspection	Present	Mouth Kiss	Opposite	
D – Ki	1	1	0	0	0	0	0	0	2
D – Ke	0	0	0	0	3	1	0	0	4
D – Y	0	1	0	0	1	0	0	0	2
D – Ka	6	0	1	0	1	0	0	0	8
D – B	60	5	1	0	0	2	0	1	69
D – J	15	1	0	0	0	0	0	0	16
Ki – Ke	13	1	4	0	7	2	0	0	27
Ki – Y	23	25	0	0	3	0	1	39	91
Ki – Ka	0	0	0	0	0	5	0	0	5
Ki – B	6	9	3	0	0	0	0	0	18
Ki – J	7	7	0	0	0	8	0	0	22
Ke – Y	29	36	4	1	0	0	0	28	98
Ke – Ka	0	0	0	0	0	1	0	0	1
Ke – B	5	18	16	0	5	0	0	0	44
Ke – J	0	2	0	0	0	0	0	0	2
Y – Ka	4	2	0	0	0	0	0	0	6
Y – B	21	22	2	0	0	0	0	22	67
Y – J	1	6	0	0	0	0	0	0	7
Ka – B	7	10	1	0	1	0	0	0	19
Ka – J	0	0	0	0	0	0	0	0	0
B – J	0	8	1	0	0	0	0	0	9
Total	198	154	33	1	21	19	1	90	517

Table 3a. All socio-sexual behaviours for each dyad in the Twycross group (frequency of each type).

Within the Twycross group the dominant female Diatou and low ranking female Banya were very frequent socio-sexual partners. This was most frequently initiated by Diatou who often appeared to ‘grab’ Banya and proceeded to dorso-ventral mount her, often pelvic thrusting as a male would do, as opposed to the usual side to side GG rubbing motion. Diatou was very infrequently observed to GG rub in this side to side motion as observed in the three other females and those in the Planckendael group. Diatou’s socio-sexual initiation with Banya often occurred during feeding, but never resulted in food exchange or agonism and no agonistic interaction was observed between them.

Kakowet II, the dominant male, was surprising in his relative infrequency of socio-sexual behaviour. Out of 517 occurrences of socio-sexual behaviour within the Twycross group, Kakowet II was only involved as an initiator and/or receiver in 42 of these interactions. The most frequent was dorso-ventral mounting with 17 occurrences, followed by ventro-ventral with 12 occurrences. Socio-sexual mounting between Kakowet II and Diatou, the dominant female was, apart from two occasions, dorso-ventral and initiated by Diatou in all but one occurrence. Conversely with the young adult female Banya, the highest frequency of occurrences was ventro-ventral and largely initiated by Kakowet II. This suggests a dominance issue and possible personal preference for a particular socio-sexual type, with Diatou possibly 'preferring' dorso-ventral and Kakowet II ventro-ventral, although individuals appear to alter position according to the particular individual the socio-sexual contact is with. Interestingly Kichele, Diatou's eldest daughter and a young adult, never initiated socio-sexual behaviour with or was initiated by Kakowet II, despite being unrelated. The bonobo keeper informed me that Kichele 'behaved' as though Kakowet II was her father, and he as though she was his daughter, (Kichele arrived as a juvenile with her mother), and therefore incest avoidance may explain this. The only time I observed Kichele interacting in a socio-sexual context with Kakowet II was when he was dorso-ventral mounting her mother Diatou, and Kichele was observed to stand and present to him, her genital region up against his back.

The second adult male Jasongo, a young adult, had a similar frequency of socio-sexual behaviour to Kakowet II although slightly higher. With Diatou dorso-ventral mounting was the preferred socio-sexual position, again as with Kakowet II, Jasongo was almost equal initiator and receiver, whereas ventro-ventral mounting occurred only once and was initiated by Diatou. For Banya the results were opposite, no dorso-ventral mounting occurred between her and Jasongo, only ventro-ventral and initiated slightly more by Jasongo. Jasongo and

Kichele had equal occurrences of dorso-ventral and ventro-ventral mounting and both were equally the initiator and receiver of these contacts. As can be seen from the descriptions there are no obvious patterns at all, with all three adult females having different frequencies and types of socio-sexual behaviour with the adult males.

Ke Ke had a relatively limited number of individuals available for socio-sexual interaction (both kin and non kin), but he had by far the most socio-sexual interactions of any of the three males in the Twycross group (34% of all sexual interactions). Ke Ke and his mother Diatou had no dorso or ventro-ventral mounting interactions, the only socio-sexual contact involved brief genital inspections by Ke Ke, often while grooming. With Kichele, Ke Ke's half sister, mounting socio-sexual behaviour did occur, all initiated by Ke Ke, but usually prevented by Kichele. Kichele would sit down; push Ke Ke away or on some occasions if Ke Ke persisted, threaten and attack him. All but one of these socio-sexual interactions was dorso-ventral and usually in a feeding situation where Kichele was feeding. Ke Ke's main focus for socio-sexual interaction was Banya, the only unrelated female in the group and the lowest ranking adult female. The majority of such interactions were ventro-ventral mounts, most frequently initiated by Ke Ke, although Banya did initiate occasionally. Dorso-ventral mounts also occurred, though much less frequently and only initiated by Ke Ke.

Diatou and her daughter Kichele had very little socio-sexual contact, only one occurrence of dorso-ventral and ventro-ventral mounting was observed. Diatou initiated socio-sexual contact on both these occasions and the absence of socio-sexual behaviour generally was possibly due to both individuals being close kin and therefore a reduced frequency of tension and dominance interactions. Diatou and Banya had a lot of socio-sexual contact and the most frequent type was dorso-ventral, initiated by Diatou (over 50 occurrences) Diatou would appear to actively seek out Banya, who often appeared unaware of

Diatou until Diatou grabbed a leg or arm. Diatou was observed to move some distance to initiate socio-sexual contact, particularly during feeding and this sometimes involved going outside or inside to Banya, when Diatou was in another part of the enclosure.

Socio-sexual interactions between the two young females, Kichele and Banya, were also infrequent and no clear pattern occurred. Both dorso-ventral and ventro-ventral mounts occurred and were initiated and received by both individuals, although Kichele initiated socio-sexual contact more frequently and Banya was most often the receiver. Therefore the dominant individual, Kichele, like her mother Diatou, initiated more than the subordinate individual, Banya. Other socio-sexual behaviours were much less frequent, only genital massage, self-genital massage, genital inspection and opposite having more than a few occurrences. Opposite was observed and initiated largely between Yasa and either Kichele, Ke Ke or Banya and would involve Yasa in the top position facing away from the individual, normally lying horizontally.

Towards the end of data collection Banya gave birth to her first infant, a female, later named Kya. This was quite unexpected and I arrived as planned the following day to this new arrival. Diatou was carrying the infant and during the next 3-day period of observations Banya was not observed to interact with the infant in any way. What was interesting was that during this 3-day period Diatou initiated socio-sexual contact with this infant on 4 occasions, all ventro-ventral with the infant clinging low down on Diatou's body. Diatou was observed to attempt to GG rub, with a rhythmic side-to-side motion, as opposed to her usual pelvic thrusting. Each time this took place Diatou held the infant with one hand while looking down at it the whole time. I have not seen any reports of this occurring with such a young infant, but can only assume that this was a normal occurrence. Diatou was not the infant's biological mother and therefore this makes it more difficult to analyse.

3.2 Self-genital massage in both groups

	Diatou	Kichele	Ke Ke	Yasa	Kakowet	Banya	Jasongo
Total	21	77	9	8	1	1	1
Percentage	17.8%	65.3%	7.6%	6.8%	0.8%	0.8%	0.8%

Table 3.b Self-genital massage occurrences for the Twycross group.

	Hermien	Hortense	Redy	Kidogo	Vifijio	Zomi	Zamba
Total	0	1	5	1	3	112	14
Percentage	0%	0.7%	3.7%	0.7%	2.2%	82.4%	10.3%

Table 3.c Self-genital massage occurrences for the Planckendael group

In the Twycross group the most frequent individual to self-genital massage was the young adult female Kichele, accounting for 65.3% of all occurrences. The juvenile female in that group, Yasa only accounted for 6.8%. Kichele would particularly self-genitally massage at feeding times and would often use objects like a plastic bin or ball to rub against. The adolescent male Ke Ke only accounted for 7.6% of all self-genital massage and rarely used objects while doing so. The results from both groups tend to reflect those found in de Waal's study, that self-genital massage occurred mostly by adolescent males, females and juveniles (1995:44). In both groups adult males self genitally massaged the least out of all the age/sex groups.

Zomi was responsible for 82.4 % of all self-genital massage in the Planckendael group with 112 separate occasions, far exceeding any other individual in either group. The other juvenile, Zamba accounted for 10.3% of all self-genital massage, so between them the juveniles had 92.7% of all self-genital massage in the group. This is particularly surprising given the data was collected in the space of 6 days. Zamba and Zomi in particular would often

carry a plastic bottle or similar object and periodically rub their genitals on this object, often several times in succession. Zamba could be seen to either insert his penis into the bottle opening or place the bottle onto his penis and then thrust. This behaviour was also observed in Vifijio and Redy, Zamba's older brothers, but not in any other individuals in Planckendael or any of the males in the Twycross group. Self-genital massage using the feet was observed in most male bonobos, Ke Ke and Kakowet II from the Twycross group and Zamba and Vifijio from the Planckendael group. Both feet would be clasped around the erect penis and rhythmically rubbed, adult male bonobos were generally not observed doing this, apart from Kakowet II. Females would use an inanimate object like a ball or their hand to self-genital massage. I did occasionally observe females using a foot to self-genital massage, but a foot was more frequently used to genitally massage another individual. An interesting observation involved Diatou, the dominant female in the Twycross group, taking Banya's foot and using it to self-genital massage. I have not observed this behaviour before or since. I also observed on 5 occasions in the Twycross group the female Banya to genitally massage the adolescent male Ke Ke using her foot. This occurred usually when Ke Ke was pestering Banya and appeared to be a tension reduction mechanism when Banya did not want Ke Ke to mount her or during feeding because following these genital massages Ke Ke stopped pestering and moved away.

3.3 Socio-sexual behaviour in the Planckendael Group

Fewer socio-sexual interactions were observed within the Planckendael group than those of the Twycross group due to the amount of time available for observations, but they do provide a useful comparison to the Twycross group and an indication of the socio-sexual behaviours that occurred in this group.

The dominant young adult male Redy had relatively frequent socio-sexual behaviour within the group. Redy initiated with all group members apart from Hortense, his mother, and Kidogo the other adult male. On the other hand Redy only received socio-sexual behaviour from the two juveniles, the female Zomi and his brother Zamba. Ventro-ventral and dorso-

Socio-sexual behaviour in the Planckendael Group

<u>Dyads</u>	<u>Types of Socio-Sexual Behaviour</u>								<u>Total</u>
	<u>Dorso-ventral</u>	<u>Ventro-ventral</u>	<u>Genital Massage</u>	<u>Oral</u>	<u>Genital Inspection</u>	<u>Present</u>	<u>Mouth Kiss</u>	<u>Opposite</u>	
Dz-He	0	0	0	0	0	0	0	0	0
Dz-Ho	0	0	0	0	0	0	0	0	0
Dz-Ki	0	0	0	0	0	0	0	0	0
Dz-V	8	2	0	0	0	0	0	0	10
Dz-R	2	2	0	0	0	0	0	0	4
Dz-Zo	0	0	0	0	0	0	0	0	0
Dz-Za	0	0	0	0	1	0	0	0	1
He-Ho	6	2	1	0	0	0	0	0	9
He-Ki	0	0	0	0	1	0	0	0	0
He-V	0	0	0	0	1	0	0	0	1
He-R	1	1	0	0	0	0	0	0	2
He-Zo	0	3	0	3	0	0	2	0	8
He-Za	0	0	0	0	0	0	0	0	0
Ki-V	2	0	0	0	0	0	0	0	2
Ki-R	0	0	0	0	0	0	0	0	0
Ki-Zo	0	0	0	0	0	0	0	0	0
Ki-Za	0	0	1	0	0	0	0	0	1
V-R	0	0	0	0	0	0	0	0	0
V-Zo	1	2	1	0	0	0	0	0	4
V-Za	0	1	0	0	0	0	0	0	1
R-Zo	15	12	0	0	0	0	0	0	27
R-Za	0	0	0	3	0	0	0	0	3
Zo-Za	9	14	0	1	0	1	2	0	27
Total	44	39	3	7	3	1	4	0	100

Table 3.d All socio-sexual behaviours for each dyad in the Planckendael group (frequency of each type).

ventral were the most frequent types of socio-sexual behaviour; self-genital massage occurred on five occasions and was the highest of all the adults. Redy's most frequent socio-sexual partner, and in fact all group members' 'favourite', was the juvenile female Zomi, and this occurred mostly in a play context. On two occasions where Redy and Zomi ventro-ventral mounted, ejaculate could be seen on Redy's belly fur and it was apparent that Redy was still fully erect following this.

The older, but subordinate adult male Kidogo had infrequent socio-sexual behaviour and interacted with the group generally very infrequently. Kidogo was observed to initiate socio-sexual contact only once, with Hermien an adult female. Kidogo was the receiver on two occasions, both to socio-sexual initiations by Vifijio, the adolescent male, who was then dorso-ventrally mounted by Kidogo. No other socio-sexual behaviour occurred except one instance of self-genital massage.

The oldest adult female Dzeeta also had infrequent socio-sexual interaction and was not observed to initiate once with any individual. Dzeeta was the most frequent receiver of all the adult females for initiations by Redy and Vifijio (dorso and ventro-ventral mounts), although there were relatively few such occurrences. Redy and especially Vifijio would usually dorso-ventral mount Dzeeta in the sitting position as Dzeeta's abnormally large genital swelling protruded. Dzeeta's genital swelling apparently changed very little and she was also never observed to GG rub with the other two females (probably extremely difficult given the immense size and weight of the swelling).

Hermien, an adult female and the mother of Zomi, relatively frequently initiated and received socio-sexual behaviour. Hermien was only observed to initiate socio-sexual contact with Hortense, another adult female, or Zomi her daughter. Hortense and Redy were the most frequent initiators of socio-sexual contact with Hermien, mainly dorso-ventral or ventro-

ventral mounting. For Redy especially, Hermien was the only female he could mate with, Hortense was his mother and Dzeeta was too old, and he spent a considerable amount of time interacting with Hermien and her daughter. Socio-sexual behaviour between Hermien and her daughter Zomi was varied, 3 occurrences of ventro-ventral mounting were observed, with 3 occurrences of oral sex (Zomi's clitoris put into Hermien's mouth). This was the only time I observed such behaviour in either group. Two occurrences of mouth kiss between this pair were also observed while playing.

Hortense was the third adult female and had three sons in the group, Redy, Vifijio and Zamba. Only one male Kidogo was unrelated, but Hortense and Kidogo were not observed to participate in any socio-sexual interaction except for one occurrence where Kidogo genitally massaged Hortense while she was feeding. Hortense's socio-sexual behaviour followed a similar pattern to that of Hermien; Hortense's main socio-sexual behaviour was with Hermien and her youngest son Zamba. This was most frequently ventro-ventral and to a lesser extent dorso-ventral mounting.

Vifijio, the adolescent male had a relatively high frequency of socio-sexual behaviour with a number of individuals in the group. Vifijio initiated dorso-ventral and ventro-ventral mounts and only with the adult female Dzeeta. Vifijio was not observed to initiate or receive socio-sexual contact with Hortense, his mother or Hermien the other adult female. The only male/male socio-sexual contact was as mentioned previously, dorso-ventral mounting with Kidogo. Unlike Ke Ke in the Twycross group, Vifijio had a relatively lower frequency of socio-sexual interaction overall, especially with the juveniles. In the Planckendael group there were two juveniles, yet socio-sexual interaction was very infrequent between them and Vifijio. This could possibly be because the juveniles spent a considerable amount of time with each other or their mothers. Although for Ke Ke only his juvenile sister was available, she

was slightly older than Zomi and Zamba and spent less time with her mother and a considerable amount of socio-sexual activity occurred between them.

The juvenile male Zamba had infrequent socio-sexual behaviour with Dzeeta, Redy and his mother Hortense. The most frequent socio-sexual partner was Zomi and dorso-ventral mounting was slightly more frequent than ventro-ventral mounting, almost all of these occurring during play and often while suspended off the ground. Three occurrences of oral sex were observed where Zamba initiated with Redy his brother, displaying an erect penis and thrusting in Redy's mouth, this was also during play. Two occurrences of mouth kiss were also observed between Zamba and Zomi. The most frequent socio-sexual behaviour was like Zomi, self-genital massage and this was observed on 14 separate occurrences.

Zomi the juvenile female was by far the most sexually active individual in the Planckendael group and especially regarding self-genital massage where 112 separate occurrences were observed. Frequently, as previously mentioned, Zomi would find a plastic bottle and GG rub herself on this, often several times in succession and her clitoris visibly enlarged during such occasions. Redy was the most frequent socio-sexual partner, followed by Zamba. For Redy ventro-ventral mounting was most frequent socio-sexual behaviour, closely followed by dorso-ventral mounting, whereas for Zamba it was the opposite.

Infrequent socio-sexual behaviours such as oral sex and mouth kiss most frequently occurred between the younger individuals, often in a play context, or between a mother and her infant. Oral sex only occurred once in the Twycross group and that was between the juvenile female Yasa and her adolescent brother Ke Ke. In Planckendael oral sex occurred on 7 occasions, between the two juveniles Zomi and Zamba and between Zamba and his adolescent and young adult brothers, Vifijio and Redy respectively and between Zomi and her mother Hermien.

Mouth kiss was only observed once in the Twycross group between the juvenile female Yasa and her older sister, the young adult Kichele. Given the large difference in observation time between the two groups (36 ½ hours at Planckendael and 143 hours at Twycross) it is perhaps surprising that the individuals in the Planckendael group exhibited a relatively high frequency of oral sex and mouth kiss when compared to the Twycross group.

Another infrequent socio-sexual behaviour observed in both groups was nipple rubbing. This was a behaviour that is described only by de Waal (1995) and he suggests this has a self-reassurance function around tense events. De Waal found that almost all of the occurrences were due to one adolescent male (1995:45). From my observations and discussion with the bonobo keeper at Twycross, nipple rubbing also appeared to occur in stressful situations such as agonistic behaviour, but also when the keeper appeared, only less frequently (pers. comm). In the Twycross group only two individuals were observed to exhibit this behaviour, the dominant female Diatou and the dominant male Kakowet II, and only towards the end of data collection when tension was increasing in the group, again supporting the idea that this activity is tension related. Kakowet II was seen only to nipple rub during this period when he was in conflict with his son Ke Ke and Diatou and could be seen during an agonistic interaction to nipple rub while screaming and very agitated. Diatou would also do the same. In the Planckendael group nipple rubbing was observed on five separate occurrences, four when Hermien and Hortense would sit or stand side by side and Hermien would put her arm around the back of Hortense and rub her nipple and breast. Hortense was not observed to nipple rub Hermien and all occurrences resulted from tension due to Redy (Hortense's son) pestering Hermien. The other occasion was Hortense self-nipple rubbing in apparent frustration at being unable to access some food, which Hermien had possession of.

Therefore we see that although socio-sexual behaviour data was limited for the Planckendael group, a similar pattern occurred to that of the Twycross group. Dorso-ventral,

followed by ventro-ventral were the most frequency socio-sexual behaviours and other types were much less frequent. Male/male socio-sexual behaviour was slightly higher in frequency and range of behaviour types than for Twycross.

3.4 Agonistic interactions in both groups

Agonistics interactions were generally infrequent in both groups, although towards the end of data collection in the Twycross group agonism increased due to a change in group dynamics. Several females attacking males was not reported for the Twycross group because multiple mature adult females were not present then, but my observations confirm single attacks or occasionally a pair of females did attack males, and both the adult males Kakowet II and Jasongo were bitten, usually on the toes, fingers and legs, on several occasions. The dominant female Diatou would especially attack the younger male Jasongo, who was the frequent target for her agonism. On several occasions the young adult female Banya was seen to attack Ke Ke, the adolescent male son of Diatou, after he had been pestering her for some time and on more than one occasional bite marks were seen, usually on the limbs, hands or feet. Ke Ke had been pestering Banya for some months and at times Banya retaliated and attacked Ke Ke who always fled out of the way. Diatou did not often intervene in such situations and was never seen to attack or threaten Banya, and only occasionally Ke Ke. Kakowet II on the other hand was observed to intervene and often supported Banya in agonistic interaction against Ke Ke (although she usually managed this on her own). This was when Diatou would attack Kakowet II, supporting her son in agonistic interactions against him. Diatou and Kakowet II were previously quite close, often spending time together grooming and I had never previously seen agonism between them. Kakowet II was visibly distressed, screaming and fleeing, often to briefly make socio-sexual contact with Banya or Yasa, he also began to 'nipple rub' quite a lot, something I had not previously observed

Kakowet II to do. Diatou, although the dominant member of the group, also appeared extremely distressed by the situation, Ke Ke was her son and as such she always supported him in agonistic interactions against Kakowet II, but Diatou also was close to Kakowet II and could be seen in between them screaming and looking in both directions as if unsure what to do. Given the small group size, and that it mainly consisted of kin, agonistic interactions were particularly difficult to analyse. For example, Kichele remained neutral in most conflicts involving Ke Ke, Banya and Kakowet II and only assisted Diatou in agonistic interactions against Jasongo. As Kichele was the second most dominant female, the lack of support from Kichele did little to resolve the conflict between Ke Ke, Diatou and Kakowet II. With several other adult females, as would occur in the wild, Diatou would probably have been supported and able to resolve the situation and Kakowet II would have been able to get away. Clearly in such situations captivity creates different stresses than would occur in the wild and may therefore affect socio-sexual behaviours, which evolved under different circumstances.

Agonistic interactions for the Planckendael group were very infrequent and therefore data were insufficient for analysis. Of the few agonistic interactions observed it was clear that Kidogo was the lowest ranking individual in the group by his avoidance of social interactions generally. Redy was definitely the dominant male and higher in status than Vifijio, his younger brother and Kidogo. Kidogo in particular appeared to actively avoid close contact with Redy, preferring to be as far away in distance as possible. Regarding the adult females in the group dominance was unclear, as no agonistic interactions occurred between them. From the monopolization of food Hermien appeared to be the most dominant individual, followed by Hortense and Dzeeta. Dzeeta was very slow and withdrawn following a stroke (pers. Comm.) and as such remained in the background for much of the time, therefore her status in the group can only be assumed. Dzeeta was cited as the dominant female (Vervaecke et al 2000) although the research was taken from 1995 to 1997 before Dzeeta's stroke. Dzeeta was

observed to threaten and chase Redy on one occasion where Redy attempted to grab some food from close to Dzeeta. Dzeeta, although usually quite slow, chased and attacked Redy, biting his foot, which was seen to be bleeding several minutes later. Agonism directed towards visitors and people observing was not witnessed during my observation.

Agonistic interactions in both groups were relatively low in frequency, although increasing slightly towards the end of data collection in the Twycross group due to dominance struggles. Females agonised males far more frequently than males did females.

3.5 Food Contexts

In the Twycross group regular contact with the bonobo keeper enabled me to find out possible new foods and ways of introducing food to the group. This was attempted because usually food was placed into the enclosure within easy access, and quite frequently socio-sexual behaviour or any social behaviour was limited and feeding competition minimal. Coconuts for example were suggested in order for the individuals to have some mild competition, which would hopefully result in increased socio-sexual behaviour, and this worked initially, but food exchange did not occur. Also individual preferences for particular foods were apparent and this further reduced competition. Insect foods were also mentioned but this group would not eat any insects offered and had been tried previously, and when the occasional insect came into the enclosure it was either ignored or 'flicked' out of the way. On one occasion the adolescent male Ke Ke together with Yasa caught a young starling, but no attempt was made to eat this bird and eventually it was discarded (by then already dead).

The Planckendael group appeared to have more feeding opportunities throughout the day, with willow branches regularly offered mid morning tied together in bundles, which the adult females immediately took possession of, and the males collected what was dropped. These branches kept the group occupied for some time, as leaves and bark were stripped and

eaten and together with food stuffed into plastic bottles, together with wood wool (placed in a cage fixed from the roof of the enclosure) this provided a more naturalistic pattern of feeding and food competition. Interestingly this did not result in more frequent socio-sexual behaviour.

3.6 Proximity (nearest neighbour frequency).

There was found to be no correlation between proximity or nearest neighbour (NN) frequency and socio-sexual behaviour following agonistic interactions. Individuals who were frequent NN were often infrequently reconciled sexually. For both the study groups proximity or nearest neighbour analysis (NN) was most closely linked along kinship lines and/or rank and this high kinship link probably explains why there is no correlation. For the Twycross group the dominant female Diatou and her three offspring were the most frequent NN and all had very infrequent sexual reconciliation. As these individuals are all close kin, sexual reconciliation is probably unnecessary and other forms of reconciliation like grooming would occur. The lowest ranking individuals Banya and Jasongo were the least frequent NN of all the group members and were peripheral in the group generally, although all individuals in the group had relatively similar frequencies of NN scores. What was apparent from the results is that for Jasongo, although he has low sexual reconciliation levels generally, Diatou and Kichele, the dominant two females were the most frequent individuals to reconcile sexually with him. A similar pattern occurs with Banya and Kakowet II and Ke Ke reconciled sexually with Banya.

A similar pattern applied to the Planckendael group, with related individuals being the most frequent nearest neighbours of each other. Individuals with no kin in the group were often peripheral, especially Kidogo who was the lowest ranking male and spent a considerable amount of time on the periphery of the group.

I will now present the data for each hypothesis and subsequent predictions.

3.7

The Twycross Group

Hypothesis 1: Reconciliation is in the form of socio-sexual behaviours

Prediction 1: Socio-sexual behaviour follows agonistic interactions

Socio-sexual behaviour occurred in 31 instances (5.9% of all socio-sexual behaviour) following an agonistic interaction, and 6 instances (1.14%) of occurrences preceding an agonistic interaction. This was out of a total of 525 socio-sexual behaviours for the group. Of the 31 interactions whereby socio-sexual behaviour occurred following agonism, only 4 of these were between former opponents, with 21 occurrences between one former opponent and another individual and 6 between individuals, neither of which was directly involved in the agonistic interaction. Therefore the data are not as predicted, a low occurrence of socio-sexual behaviour followed agonistic interactions.

Prediction 2: Rates of socio-sexual behaviours increase after agonism

There were 43 occurrences of pre conflict and 31 occurrences of post conflict socio-sexual contacts and the average overall rate (or mean) of pre conflict socio-sexual behaviour was 0.26 and post conflict was 0.59. The rate (mean) of socio-sexual behaviour following agonism was found to be statistically highly non-significant, compared to the rate before agonism. Post conflict socio-sexual contact occurred less frequently than pre conflict socio-sexual contact. Therefore socio-sexual contacts before and after agonism are independent of one another, Fisher's Exact Test: ($P = 0.424$).

The following charts (Figures 3.i and 3.ii) show socio-sexual behaviour recorded 15 minutes before agonistic interactions and 15 minutes following agonistic interactions, together with socio-sexual behaviour recorded in a comparable time (matched time), taken 15

minutes before and after the time during the day an agonistic interaction occurred. Where possible this was the following day and in a period where no agonistic interactions were observed.

The frequency was low overall in both actual and matched samples, but in the first 4 minutes before an agonistic interaction socio-sexual behaviour was the most frequent. This appears not to be random as the matched time was more evenly distributed over the time span and only 1 occurrence of socio-sexual behaviour was observed in the first 4 minutes of comparable time. This compares to 14 occurrences in the 4 minutes preceding actual agonistic interactions.

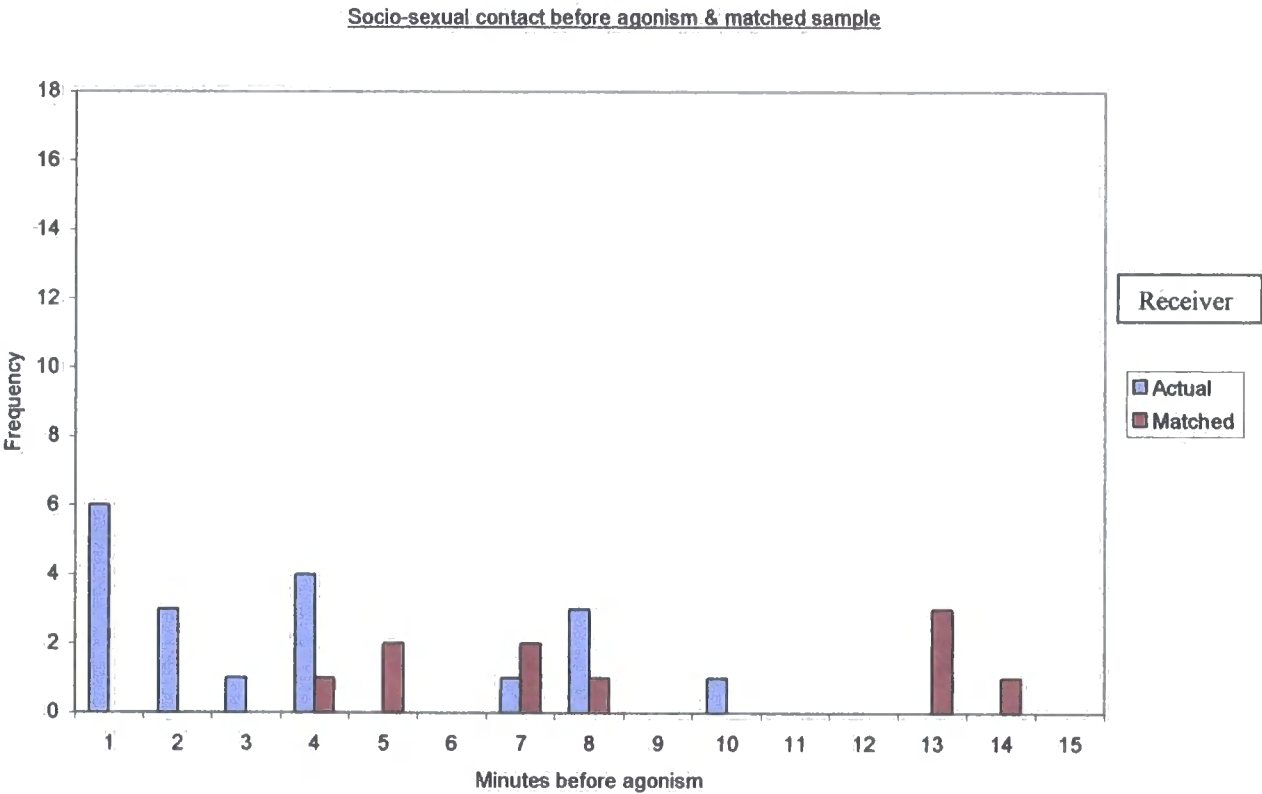


Fig. 3.i. The frequency of socio-sexual contact before agonism (in minutes), comparing both actual and a matched sample. SSB is low overall prior to agonism but is relatively concentrated in the first 4 minutes prior to agonism, whereas in the matched time this was absent.

Socio-sexual contact following agonism & matched sample

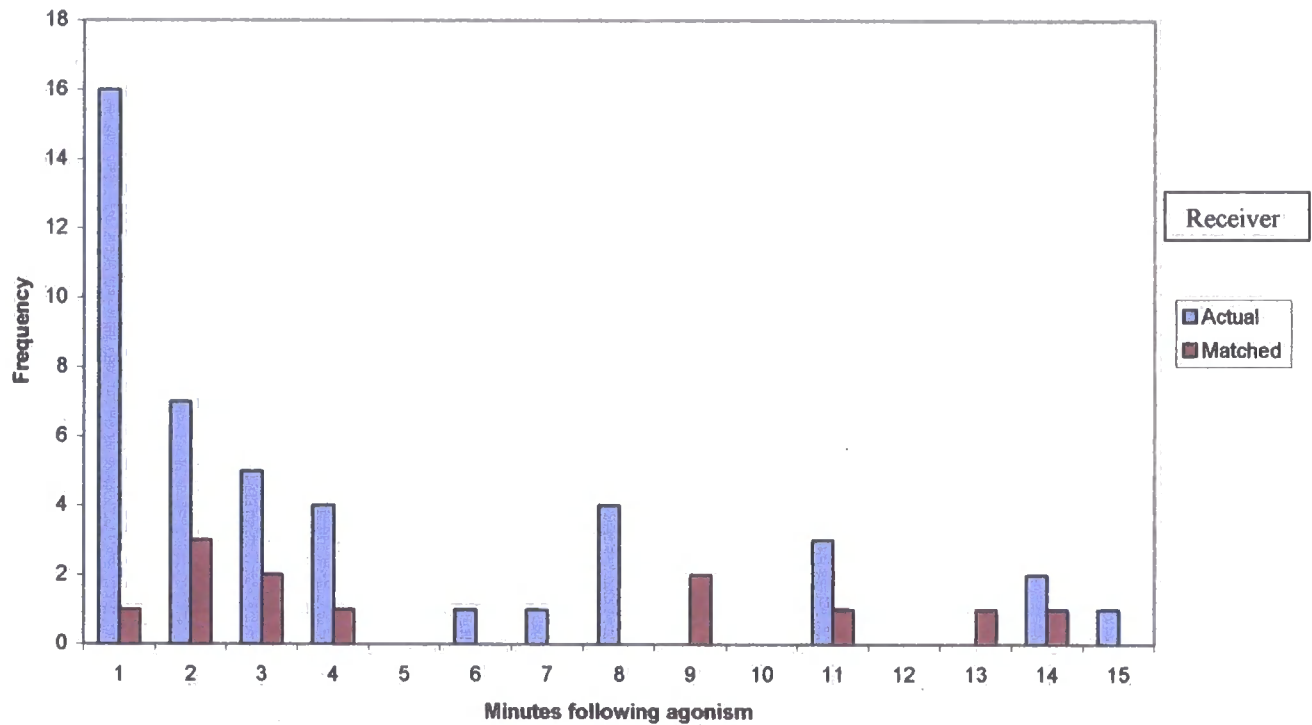


Fig. 3.ii The frequency of socio-sexual contact following agonism (in minutes), comparing both actual and a comparable matched sample. SSB is much higher in frequency overall than prior to agonism, again concentrated in the first 4 minutes prior to agonism. In the first minute following agonism SSB is most frequent, the matched sample having not apparent supporting the hypothesis that SSB are a form of reconciliation

Following agonistic interactions the difference between the actual and matched times are more apparent. Again in the first 4 minutes following an agonistic interaction this was particularly evident. 16 occurrences occurred in the first minute with only 1 in the matched sample. Therefore this supports the prediction and rates of socio-sexual behaviours increased following agonism compared to time prior to agonism.

Socio-sexual contact following agonism

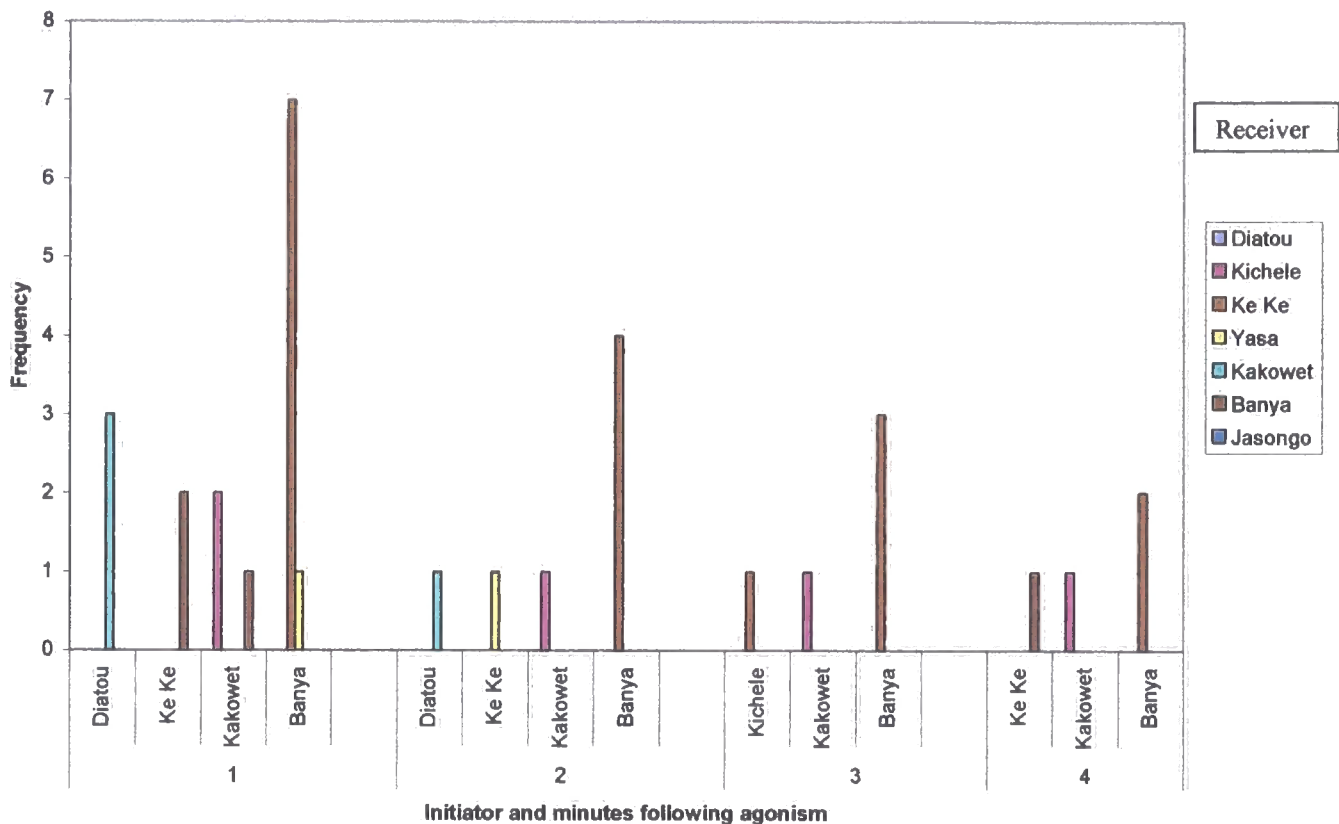


Fig. 3.iii The actual initiators and receivers in all socio-sexual contact following agonism and the minutes this occurred (first 4 minutes following agonism). This chart provides a more detailed account of individuals and SSB following agonism.

Several points are evident from this graph. Diatou, the dominant female, was only observed to actively initiate and not receive socio-sexual contact. Also this initiation was only with the dominant male Kakowet. The juvenile female Yasa was not observed to initiate in these circumstances and was a receiver only from Banya and her elder sibling Ke Ke. The most frequent initiation was between Banya and Ke Ke, mainly initiated by Banya and received by Ke Ke. This was particularly evident in the first minute following agonism. This is possibly explained by the greatest agonism being between these two individuals and although Banya is female and older than Ke Ke, she is the lowest ranking female and Ke Ke

the son of the dominant female. Kichele, Diatou’s eldest offspring and daughter, was very infrequently involved in agonism and this is reflected in only one initiation with her sibling Ke Ke and she was the receiver only from Kakowet the dominant male. This is difficult to assess because conversation with the keeper suggested that Kakowet ‘behaved’ as though Kichele was his daughter. She was introduced as an infant into the group with her mother and had grown up with Kakowet being the only adult male. Jasongo, the lowest ranking individual, was neither an initiator nor receiver in the first 4 minutes following an agonistic interaction.

Overall, out of the 74 socio-sexual occurrences, 30 were before agonism (40.5%) and 44 occurrences following agonism (59.5%). The non-occurrence of socio-sexual contact before an agonistic interaction (24 occurrences or 32.4% of the time) was much more frequent than that following agonism where only 6 occurrences were observed. Therefore where socio-sexual contact occurred prior to an agonistic interaction, overall the rate of socio-sexual contact was less than if socio-sexual contact had not occurred. Therefore the prediction was not supported. There were a total of 74 instances of socio-sexual behaviour 15 minutes before and after an agonistic interaction. To deduce whether or not there was a difference in the distribution, Wilcoxon Signed Ranks Test was used and no difference was found (Wilcoxon test: $Z = -0.522$, $N = 74$, $P = 0.602$).

Individual	Socio-sexual Behaviours				
	No. of Conflicts	Number		Rate	
		Before	After	Before	After
Diatou	16	9	5	0.56	0.31
Kichele	7	0	1	0	0.14
Ke Ke	38	19	23	0.5	0.61
Yasa	3	1	2	0.33	0.66
Kakowet II	22	3	7	0.14	0.32
Banya	33	17	23	0.52	0.70
Jasongo	9	0	1	0	0.11

Table 3.e The frequency and rate of socio-sexual behaviour before and after agonistic conflicts for each individual. Certain individuals have high frequency/rate of SSB centred around agonism (Ke Ke & Banya) others very little (Kichele & Jasongo).

Prediction 3: Individuals frequently in close proximity sexually reconcile more than individuals who are not frequently in close proximity

For this prediction there is no correlation and only an indication of the pattern between the two variables. 1) frequency of socio-sexual behaviour following agonism for each pair and 2) the frequency of time represented by nearest neighbour (NN), how frequently an individual was observed as the closest individual in the group to the focal individual at a given time. A correlation coefficient was not possible because each scatterplot was produced as a graphic representation between the frequency of nearest neighbour and frequency of socio-sexual reconciliation. The scatterplots do not show a statistical relationship, hence no p value, but a relationship of pairs. Each scatter plot shows one individual and the two variables for each possible partner in the group. The initiator and receiver of sexual reconciliation are represented as the left and right individuals in each pair. For the NN frequency the opposite occurs, the right individual in the pair being the NN to the individual on the left in the pair. The results are presented for each individual (Figures 3.1a – 3.1g).

Diatou : Comparison of Nearest Neighbour and Sexual Behaviour

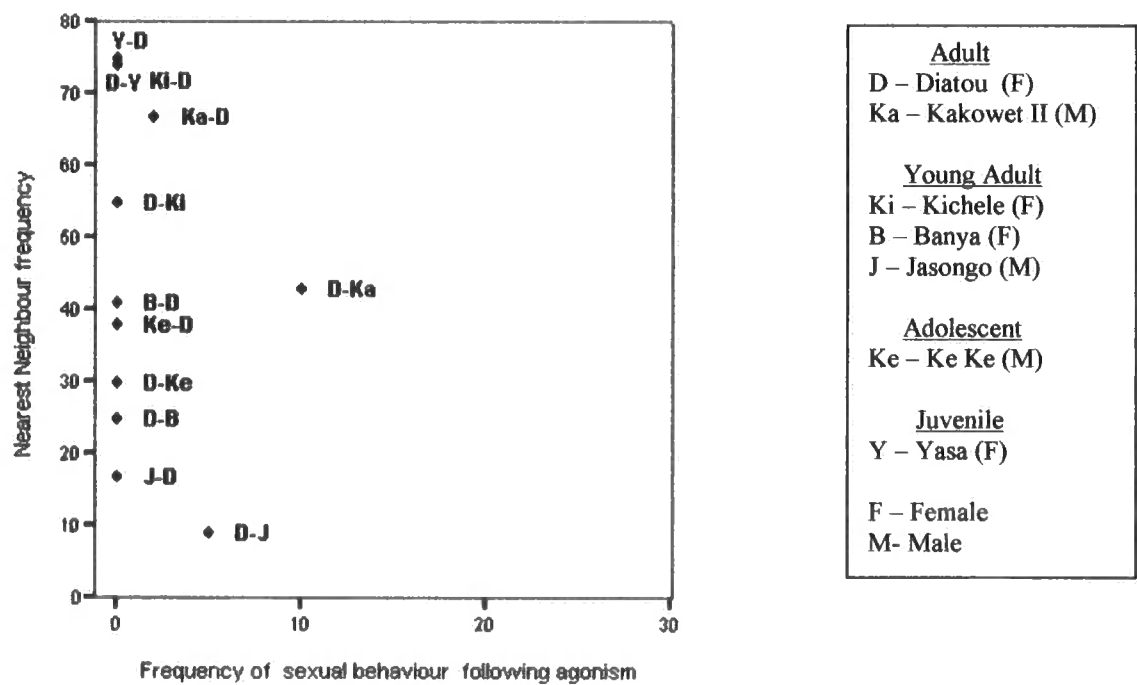


Figure 3.1a – A comparison of nearest neighbour and socio-sexual behaviour following agonism for Diatou

For Diatou the dominant female, it is apparent that the two adult males, Kakowet II and Jasongo (both unrelated to Diatou*) were the receivers and Diatou, following agonistic interactions, initiated sexual reconciliation. This applies especially to Kakowet II the dominant male, who is a frequent NN for Diatou. Jasongo on the other hand is the least frequent NN for Diatou and Yasa and Kichele the most frequent (her two daughters). The remaining individuals are to greater or lesser extents NN to Diatou but with no socio-sexual behaviour recorded following agonism. Therefore for Diatou the prediction is not supported, sexual reconciliation is not related to frequency of nearest neighbours.

Kichele : Comparison of Nearest Neighbour and Sexual Behaviour

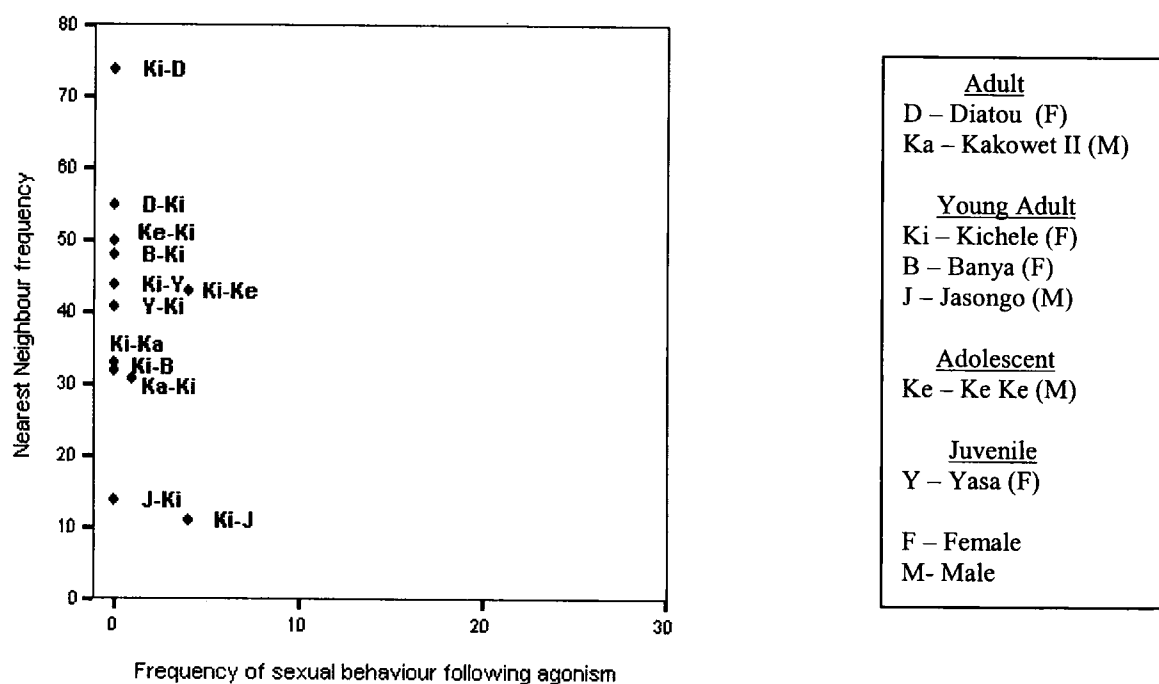


Figure 3.1b – A comparison of nearest neighbour and socio-sexual behaviour following agonism for Kichele

For Kichele, Diatou's eldest daughter, socio-sexual behaviour following agonism is also infrequent, but Kichele initiated socio-sexual reconciliation with two individuals: Ke Ke and Jasongo on four occasions. These two individuals are both a male, Ke Ke is Kichele's

half brother (this kin relationship reflects his high NN score) and Jasongo is distantly related. Socio-sexual reconciliation between these siblings was relatively high, despite Kichele being sexually mature. Jasongo was again the least frequent NN overall and Diatou the most frequent. The result is similar to that of Diatou and does not support the prediction.

Ke Ke : Comparison of Nearest Neighbour and Sexual Behaviour

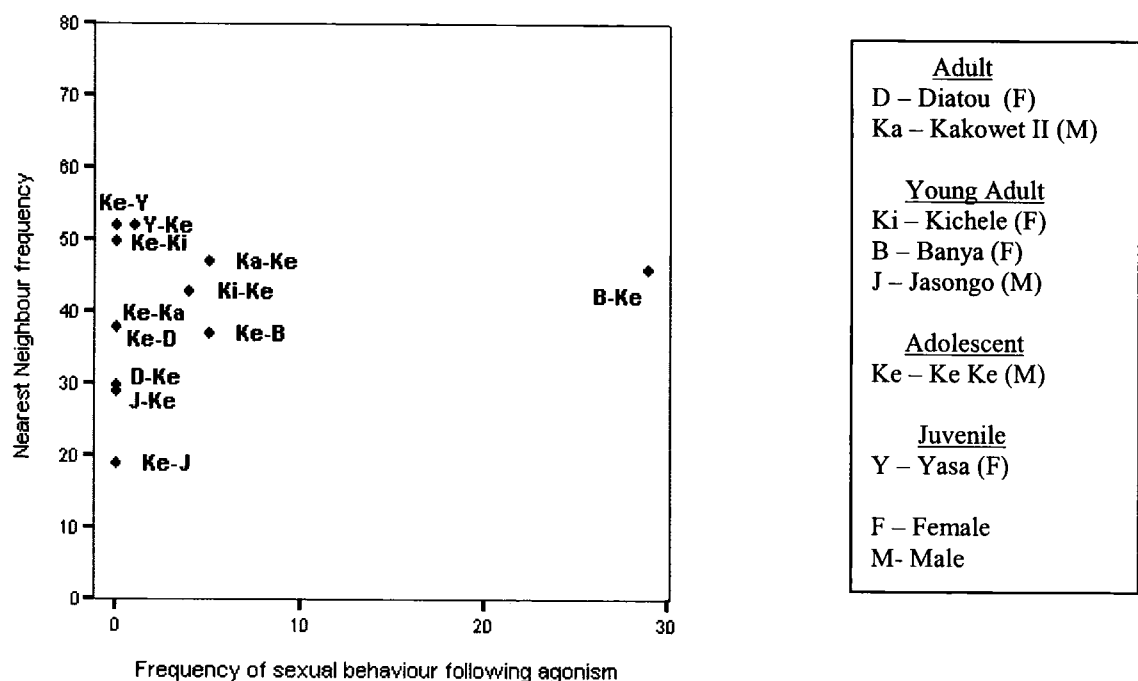


Figure 3.1c Ke Ke - comparison of nearest neighbour and socio-sexual behaviour following agonism

Ke Ke is the only adolescent in the group and son of the dominant female and the overall pattern is very different. One individual, Banya very frequently, and far more than any other group member, initiated socio-sexual reconciliation with Ke Ke on 28 occurrences. This compares with Ke Ke initiating with Banya on only 4 occurrences. Both these individuals are relatively frequent NN to each other. This high frequency of socio-sexual contact by Banya is probably due to Ke Ke’s frequent pestering of Banya and the subsequent agonistic interactions where Banya agonised Ke Ke, followed by socio-sexual reconciliation between

them. Ke Ke was more often the receiver of agonism rather than initiating it. For Ke Ke NN frequency was quite clustered, although kin were more frequent NN, namely Yasa, Kichele and Kakowet II, rather than non-kin individuals like Jasongo and kin were infrequent socio-sexual contacts and the data generally does not support the prediction. The only exception to this is Banya, both a frequent nearest neighbour and socio-sexual partner.

Kakowet II : Comparison of Nearest Neighbour and Sexual Behaviour

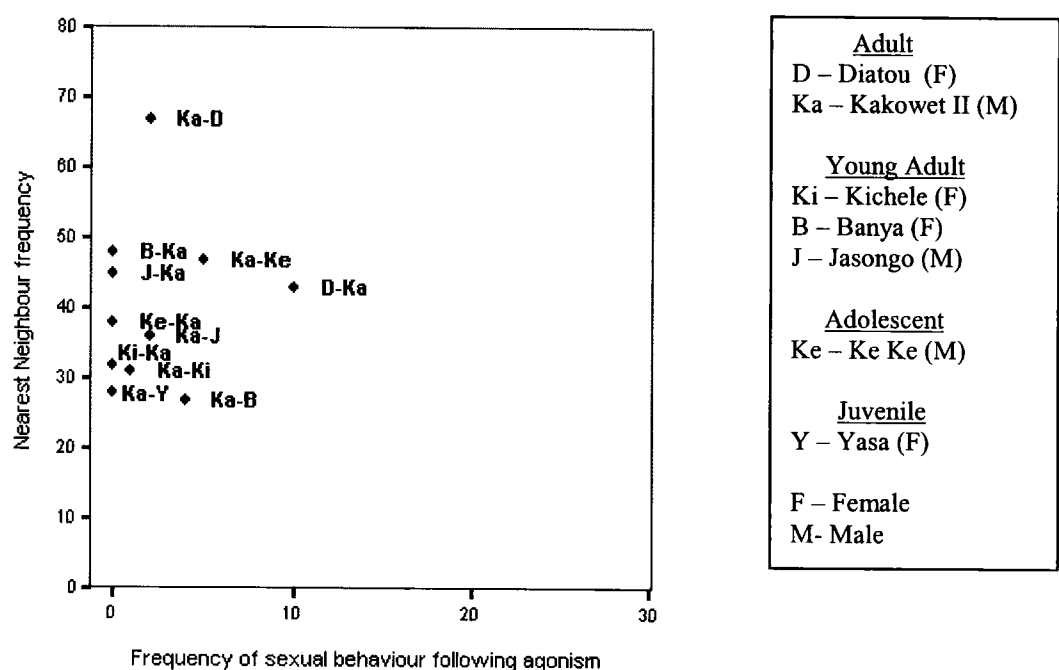


Figure 3d. Kakowet II - comparison of nearest neighbour and socio-sexual behaviour following agonism

For Kakowet II (Fig 3.1d), the dominant male, there is no real pattern at all between NN frequency and socio-sexual behaviour following agonism, with all frequencies very clustered. The only exception is Diatou, the most frequent NN but infrequent socio-sexual reconciliation by Kakowet II with Diatou and it was Diatou who initiated socio-sexual reconciliation with Kakowet II. The only two individuals Kakowet II initiated socio-sexual contact with following agonism were Ke Ke, his son, and Banya (also the least frequent NN). Banya was the only adult female Kakowet II was dominant over. Jasongo and Kakowet II

were relatively frequent NN; Kakowet II being the only individual that Jasongo was relatively a frequent NN with. Towards the end of data collection conflict between Ke Ke and Kakowet II was beginning regarding dominance in the group. Therefore for Kakowet II the prediction is not supported.

Yasa : Comparison of Nearest Neighbour and Sexual Behaviour

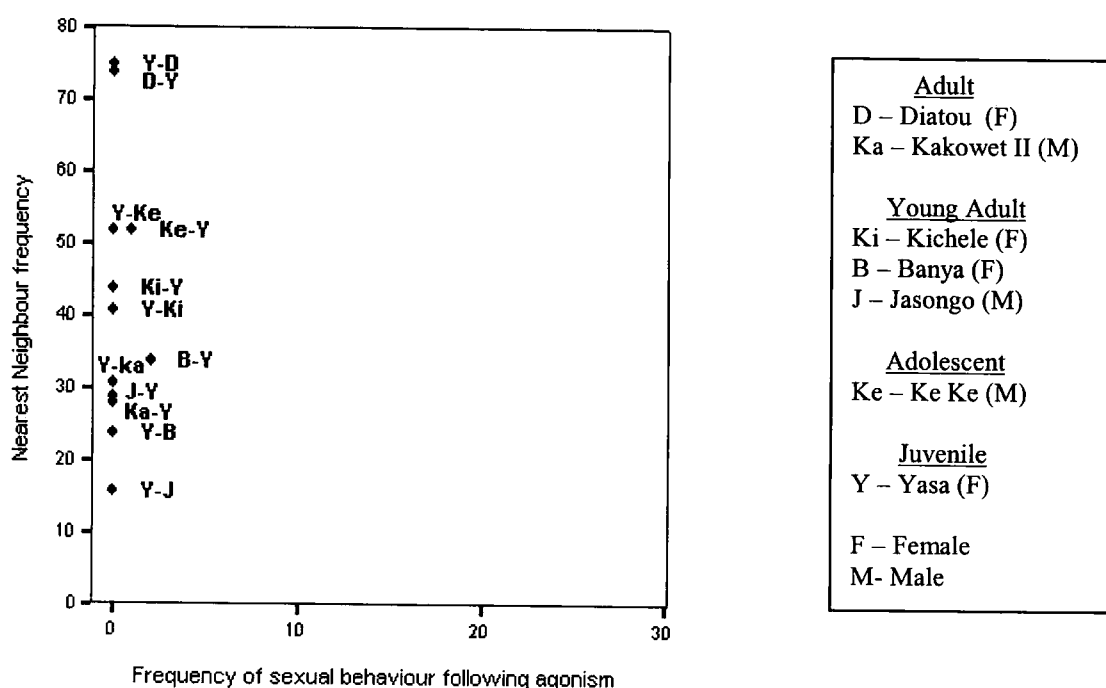


Figure 3.1e Yasa - comparison of nearest neighbour and socio-sexual behaviour following agonism

For Yasa (Fig. 3.1e), the juvenile female, there is no pattern at all probably because as the youngest member of the group she was never directly involved in any agonism. When Yasa was involved in socio-sexual contact it was only as a receiver and usually initiated by Banya and Ke Ke. Diatou was by far the most frequent nearest neighbour and Jasongo the least. For Yasa the nearest neighbour frequency was well defined in order of kin (Diatou,

Kichele, Ke Ke & Kakowet II) and non-kin (Banya & Jasongo). Therefore the prediction is not supported for Yasa.

Banya : Comparison of Nearest Neighbour and Sexual Behaviour

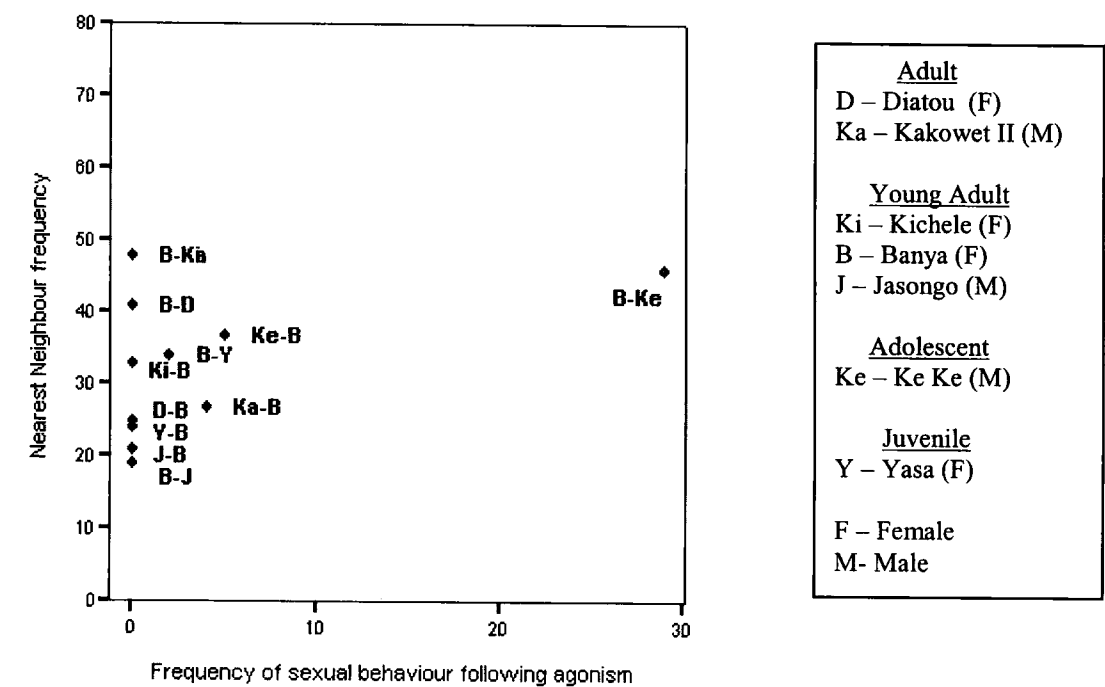


Figure 3.1f Banya - comparison of nearest neighbour and socio-sexual behaviour following agonism

For Banya (Fig. 3.1f), the only unrelated female in the group, the pattern really mirrors that of Ke Ke. Nearest neighbour frequency is low overall and clustered and again there is no relationship between the frequency of nearest neighbour and frequency of socio-sexual reconciliation. Kakowet II was the most frequent nearest neighbour and Banya would frequently sit near to Kakowet II especially when being pestered by Ke Ke as Kakowet II’s presence tended to prevent further pestering. Jasongo was the least frequent nearest neighbour. Banya initiated socio-sexual reconciliation with Ke Ke the most frequently and was the receiver of socio-sexual reconciliation by Ke Ke and Kakowet II possibly because she

was the lowest ranking adult female. As with Ke Ke, generally for Banya the prediction is not supported except for Ke Ke, who was a frequent nearest neighbour and socio-sexual partner.

Jasongo : Comparison of Nearest Neighbour and Sexual Behaviour

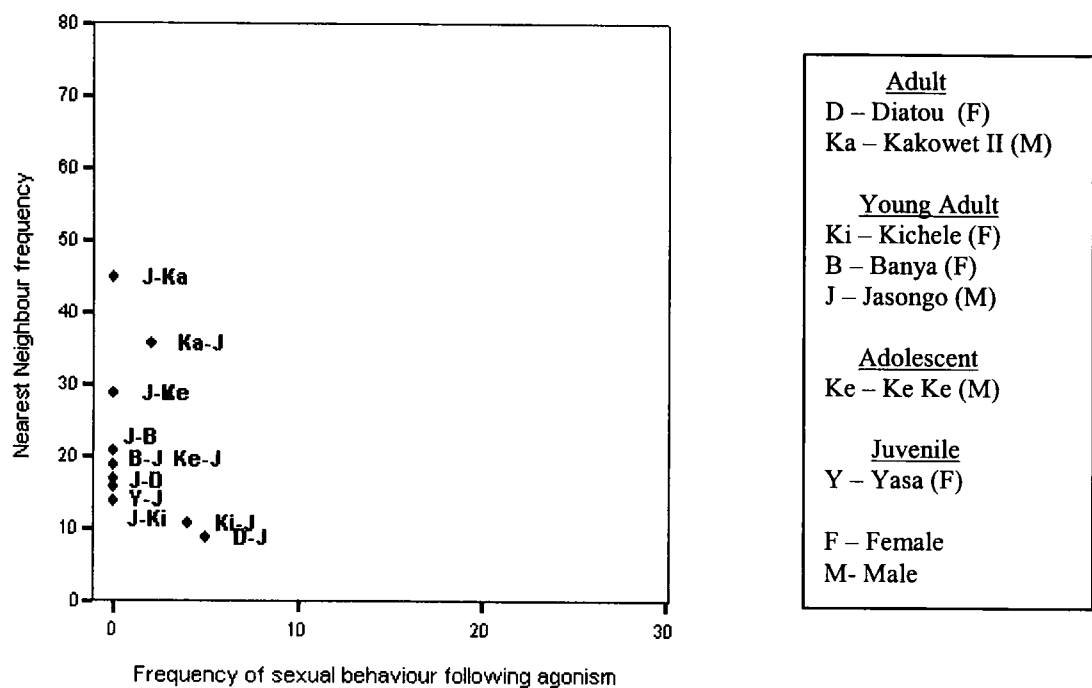


Figure 3.1g Jasongo - comparison of nearest neighbour and socio-sexual behaviour following agonism

For Jasongo, the lowest ranking group member, there was a slight relationship between NN frequency and socio-sexual behaviour following agonism. Jasongo never initiated socio-sexual reconciliation, he was always the receiver, namely by Diatou and Kichele and he was the least frequent nearest neighbour for both these individuals. Jasongo’s most frequent nearest neighbour was Kakowet II, the dominant male. It is clear from the scatterplot that the most frequent nearest neighbours are Kakowet II and Ke Ke, both males but very infrequent socio-sexual partners. Therefore the results for Jasongo do not support the prediction.

From the observations and results given there was generally no relationship between nearest neighbour frequency and socio-sexual behaviour frequency. In general kin relationships were more apparent, with close kin being close nearest neighbours and infrequent socio-sexual partners and non-kin more frequent socio-sexual partners and less frequent nearest neighbours. No statistical test was possible because there were only 7 individuals. On balance it appears that socio-sexual behaviour being a form of reconciliation was not found.

Hypothesis 2: Socio-sexual behaviours are a form of tension reduction

Prediction 1: In feeding situations socio-sexual behaviours occur more often between owners of food and bystanders than between bystanders

Out of all feeding situations observed agonistic interactions occurred on only 8 occasions, feeding was relatively peaceful and competition rare. Therefore statistical analysis between food ownership and agonism was not possible and the following analysis focuses on food ownership. Food exchange was observed very infrequently in this group and all occurrences involved Yasa, the juvenile female taking food off another individual, this occurred sporadically and with no apparent cause.

Analysis found that individuals without food (bystanders) do prefer individuals with food (owners), although the frequency of socio-sexual behaviour between individuals without food (but in a feeding context) is higher than expected. Table 3f shows that individuals who have socio-sexual contact, where both are bystanders, account for 18.5% of the total socio-sexual behaviour recorded in a feeding context. Where one individual has food and one does not this rises to 32.4%. Individuals who have food have a preference for socio-sexual contact with other individuals who also have food and this accounts for 49.1%, almost half of all such

socio-sexual behaviour. Socio-sexual contact where at least one individual has food gives a frequency of 141 out of all 173 occurrences or 81.5% of all such behaviour during feeding.

Frequency of food ownership

		Frequency	Percent	Valid Percent	Cumulative Percent
Valid	neither have food	32	18.5	18.5	18.5
	one individual has food	56	32.4	32.4	50.9
	both individuals have food	85	49.1	49.1	100.0
	Total	173	100.0	100.0	

Table 3f. Frequency of food ownership. The relationship between the possession of food and socio-sexual behaviour. There appears to be a strong relationship supporting the role of SSB in reducing tension. When both SSB partners are in possession of food this accounts for almost half of all SSB during feeding bouts.

This is significant, that food ownership is related to the frequency of socio-sexual contact in a feeding situation (Chi Sq = 24.428, df = 2, P = <0.001).

If individuals where at least one of a pair has food (owners and bystanders and both owners) are merged together and compared to bystanders where neither has food, then the result is highly significant (Chi Sq = 68.676, df = 1, P = <0.001), with individuals where at least one has food having a much higher frequency of socio-sexual contact than individuals without food.

Owners/owners and bystanders and bystanders

		Frequency	Percent	Valid Percent	Cumulative Percent
Valid	Without food	32	18.5	18.5	18.5
	With Food	141	81.5	81.5	100.0
	Total	173	100.0	100.0	

Table 3.g. As with table (3f) above, this table reflects the importance of food ownership in SSB during feeding, with 81.5% of all SSB during feeding bouts involving at least one of the dyad in possession of food.

We see that the data are as predicted, that food ownership is related to socio-sexual contact but this could also be due to other factors.

Individually the relationship between food ownership and socio-sexual behaviour, although somewhat limited, provides some interesting results illustrated below.

Diatou: socio-sexual behaviour and food ownership

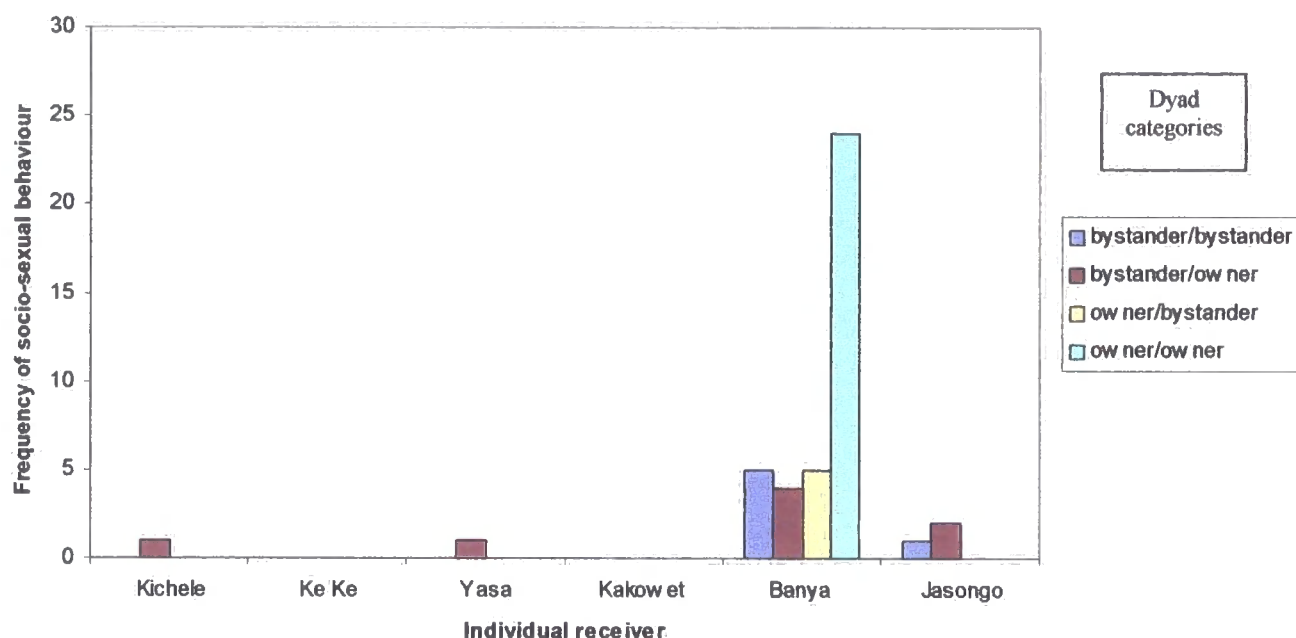


Figure 3.2a Diatou – The relationship between food ownership and socio-sexual behaviour, initiated by Diatou.

For Diatou initiation was almost exclusively with Banya and especially when both had food. Initiation with other individuals was very infrequent (1 or 2 occurrences) and non-existent with Ke Ke and Kakowet.

Kichele: socio-sexual behaviour and food ownership

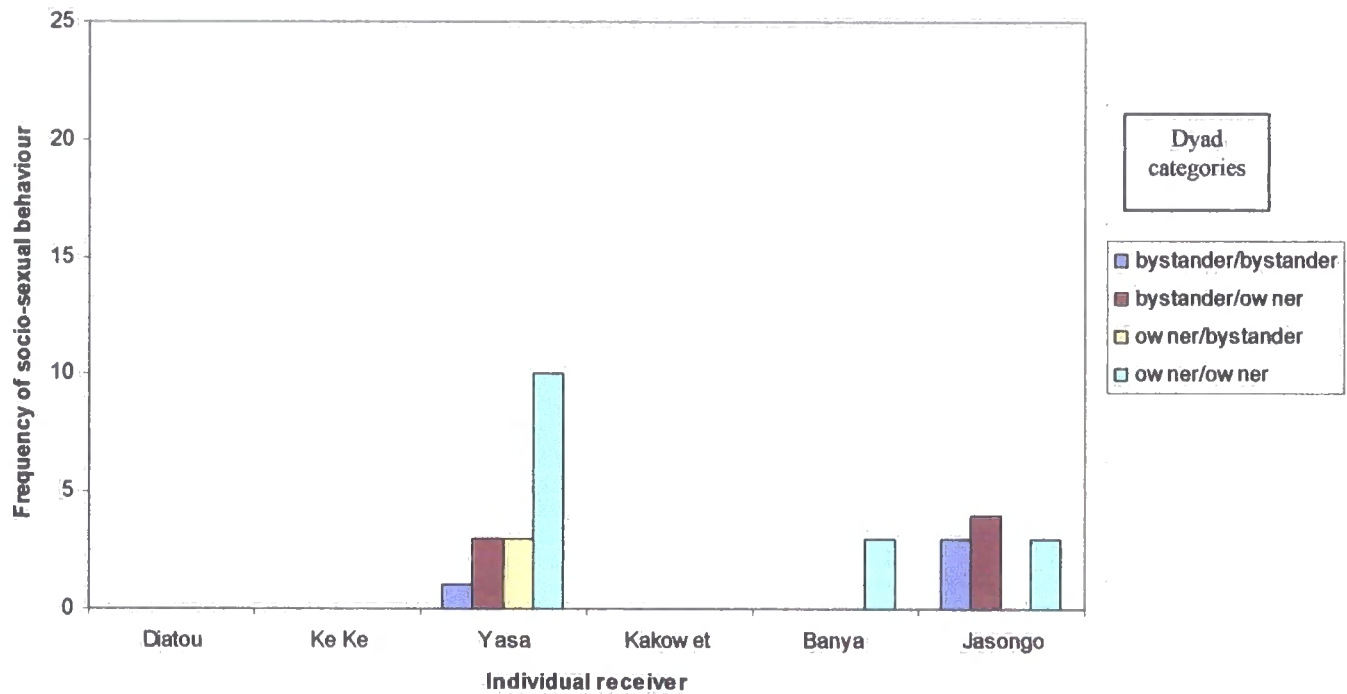


Figure 3.2b Kichele - The relationship between food ownership and socio-sexual behaviour, initiated by Kichele

Kichele also has selective initiation, namely Yasa but also Jasongo and to a lesser extent Banya. The strongest initiation frequency was again when both Kichele and the receiver had food. No initiation in a feeding bout occurred with Diatou, Kakowet or Ke Ke.

Ke Ke: socio-sexual behaviour and food ownership

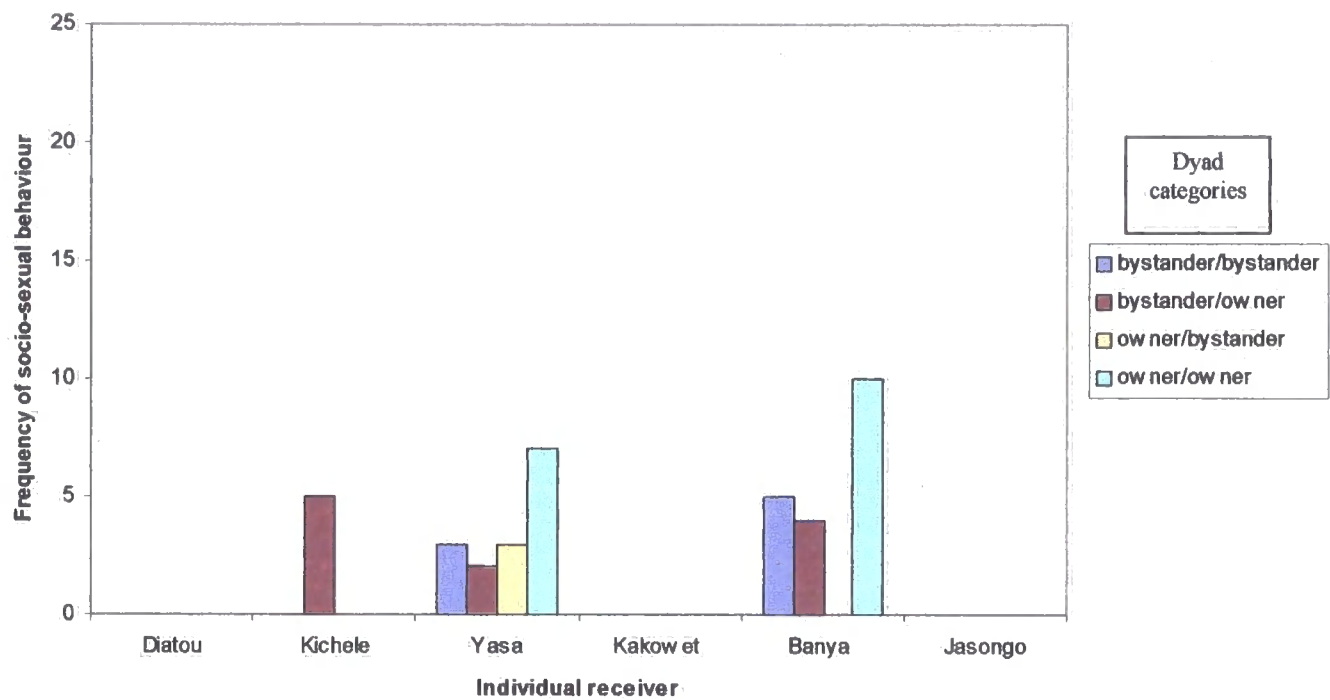


Figure 3.2c Ke Ke - The relationship between food ownership and socio-sexual behaviour, initiated by Ke Ke

For Ke Ke Banya and Yasa were the most frequent receivers of his initiation. Following the pattern seen above, this was most frequent when both individuals had food. With Kichele Ke Ke only initiated socio-sexual contact when he had no food and Kichele did.

Yasa: socio-sexual behaviour and food ownership

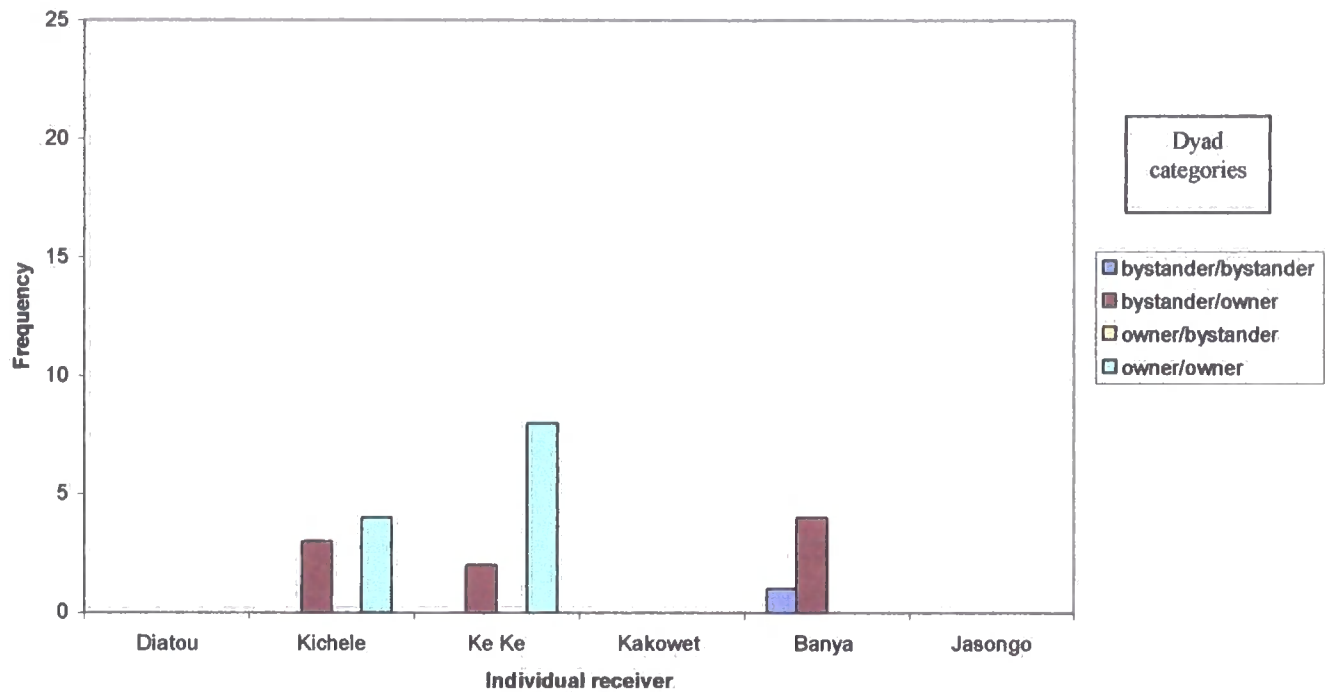


Figure 3.2d Yasa - The relationship between food ownership and socio-sexual behaviour, initiated by Yasa.

Yasa showed a preference for Ke Ke, Kichele and Banya, but with her siblings mainly when both had food or the receiver had food and Yasa did not. With Banya Yasa only initiated when Banya had food and Yasa did not.

Kakowet II: socio-sexual behaviour and food ownership

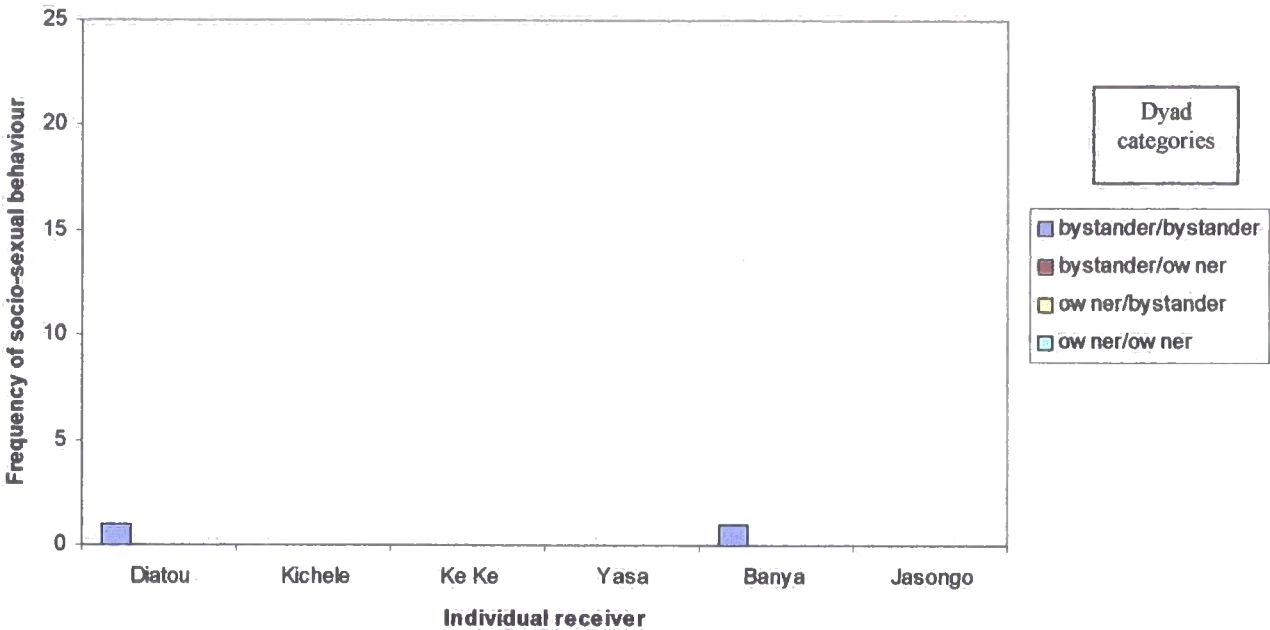


Figure 3.2e Kakowet II - The relationship between food ownership and socio-sexual behaviour, initiated by Kakowet II.

It is clear from Figure 3.2e that Kakowet initiated and received the least socio-sexual contacts during feeding of any of the individuals. Kakowet only initiated once with Diatou and Banya and only when neither initiator or receiver had food.

Banya initiated infrequently during feeding but with a preference for Diatou and Kichele, especially when both had food. No initiation was observed with Kakowet and minimal initiation with the remaining individuals.

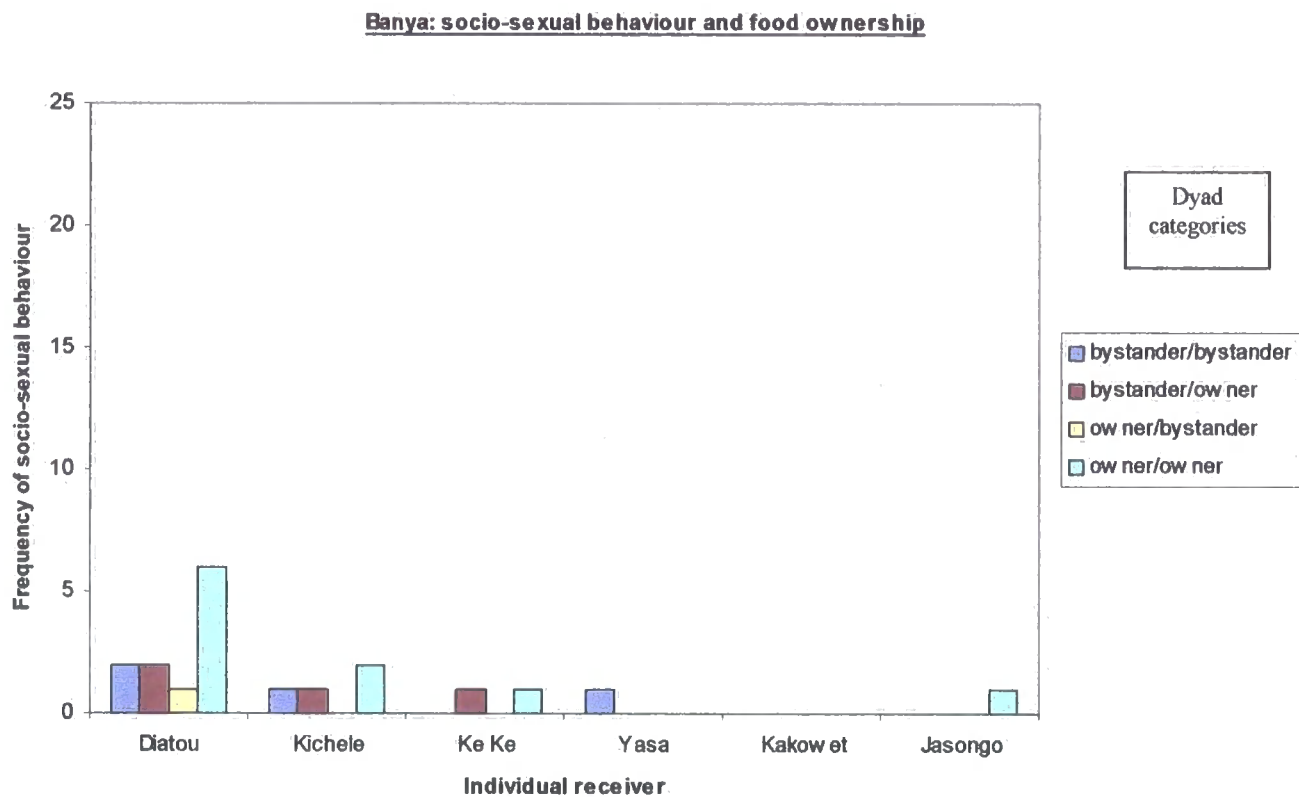


Figure 3.2f Banya - The relationship between food ownership and socio-sexual behaviour, initiated by Banya.

Jasongo: socio-sexual behaviour and food ownership

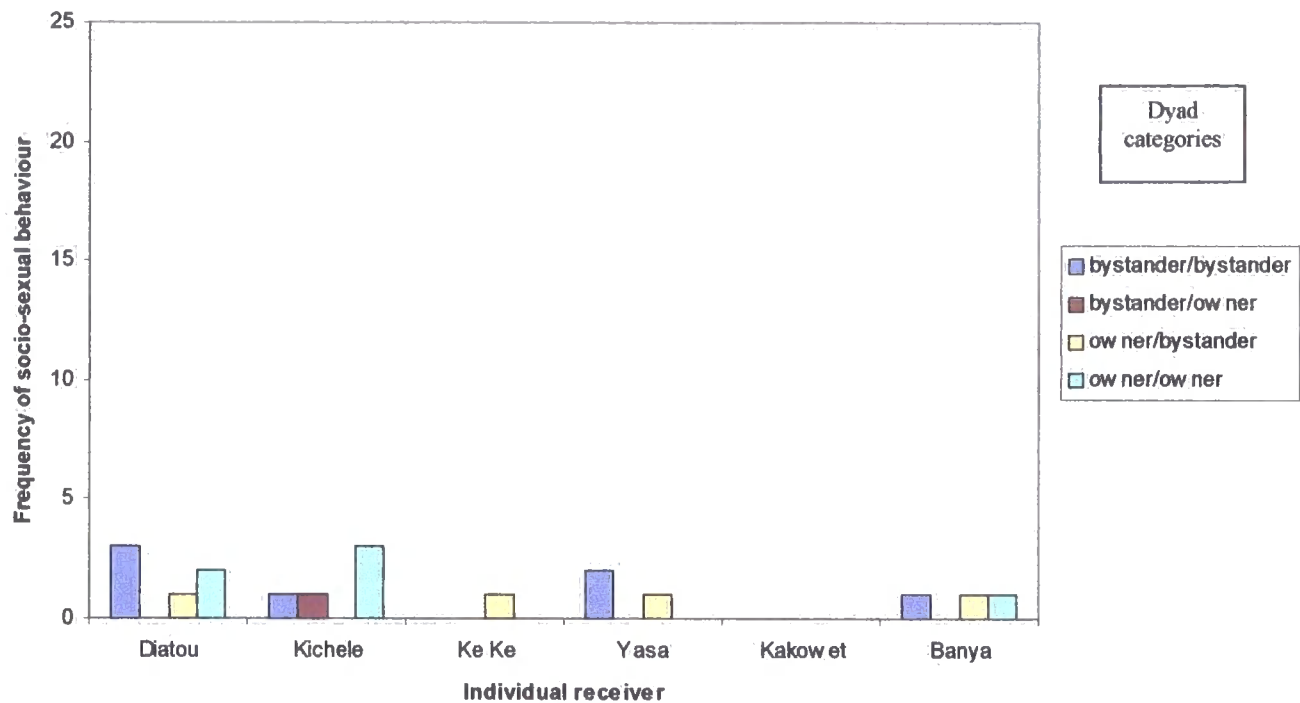


Fig 3.2g Jasongo- The relationship between food ownership and socio-sexual behaviour, initiated by Jasongo

For Jasongo socio-sexual initiation was observed with all individuals except Kakowet but there was a low frequency overall and no clear pattern or preference, although slightly more initiation with Diatou and Kichele.

The results support this prediction that socio-sexual behaviour is more frequent with individuals in possession of food than those without food.

Prediction 2: The average duration of socio-sexual contacts would be expected to be higher during feeding, where tension is high, than in a non-feeding context.

To test this prediction all socio-sexual behaviours recorded during feeding (i.e. when food was present), together with the duration in seconds were correlated for each socio-sexual contact.

There were 165 sexual occurrences during feeding and a comparable number of socio-sexual contacts from non-feeding situations that were taken randomly from all socio-sexual behaviour recorded for the group, i.e. socio-sexual behaviour at the same or similar time on the following day if possible.

The mean for non-feeding and feeding socio-sexual contacts were calculated and the results showed that on average during a feeding situation the duration of socio-sexual contacts was longer than in a non feeding context (Levine’s Test for equality of variance $T = -3.580$, $df = 291.087$, $P = <0.001$), see table (3e). The average duration of socio-sexual behaviour in a feeding context was 6.92 seconds and in a non-feeding context was 4.90 seconds. The prediction is supported by the data.

Independent Samples Test

		Levene's Test for Equality of Variances		t-test for Equality of Means		
		F	Sig.	t	df	Sig. (2-tailed)
Duration	Equal variances assumed	15.128	.000	-3.580	328	.000
	Equal variances not assumed			-3.580	291.087	.000

Table 3.h. Levene’s test for equality of variances

The following chart (Fig 3.2h) shows the duration in seconds that a socio-sexual behaviour occurred and the frequency of this occurrence. By far the most frequent duration during feeding situations was very brief, only 1 second, with a relatively gradual decrease in frequency as duration increased.

Frequency of socio-sexual behaviours (feeding bouts)

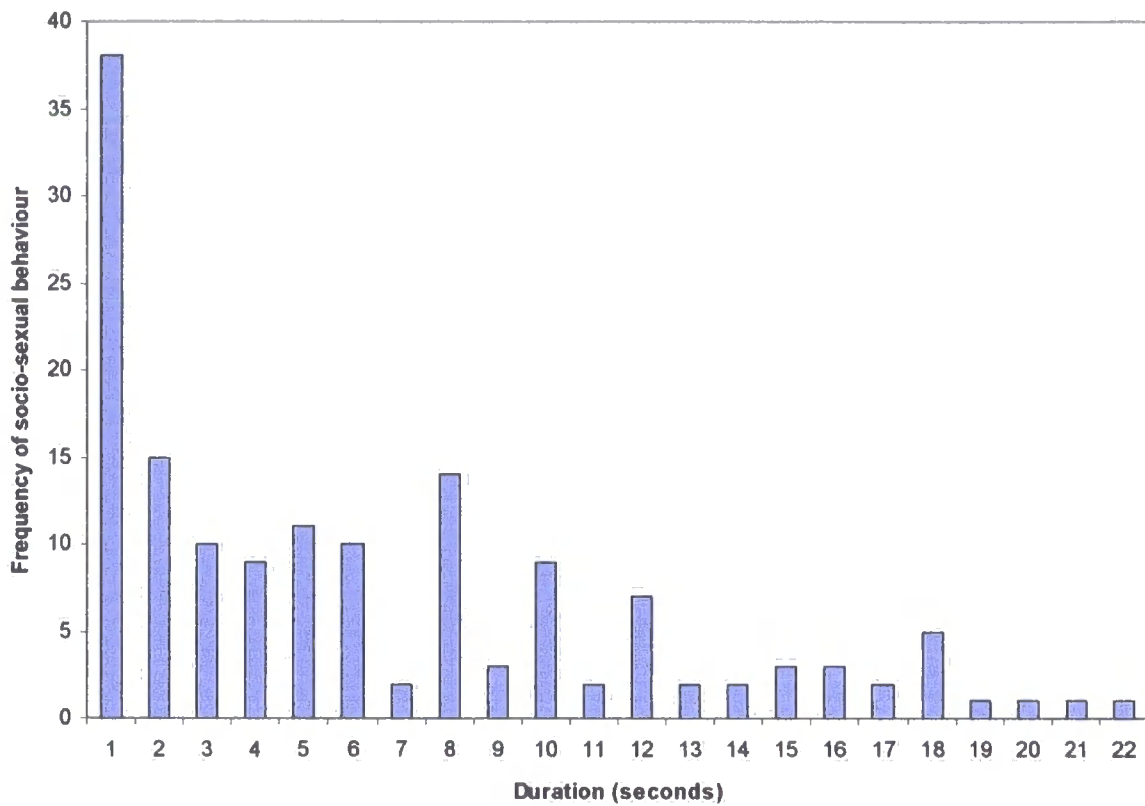


Figure 3.2h Frequency of socio-sexual behaviours during feeding bouts. The duration of all such SSB from 1 to 22 seconds was observed. The shortest duration (1 second) was the most frequent, decreasing in frequency as the duration increases.

Number of Socio-sexual behaviours per feeding bout

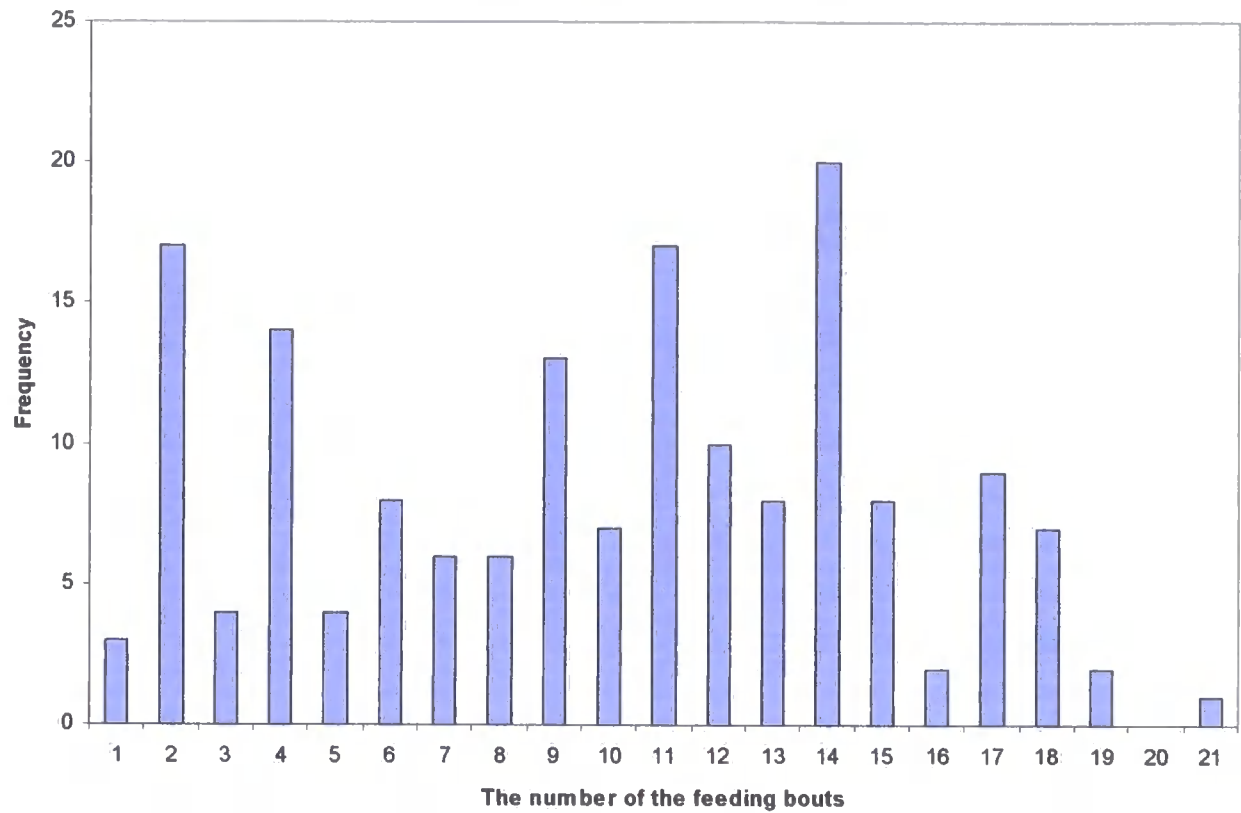


Figure 3.2j The number of SSB per feeding bout. There were 21 feeding bouts observed and the frequency of SSB varied greatly from none in bout 20 to 20 in bout 14.

In bout 1 only 3 occurrences were noted, whereas in bout 14 it was 20 occurrences.

Only in bout 20 was no socio-sexual behaviour observed during a feeding bout. The range is therefore considerable with the average frequency of socio-sexual behaviour per bout being 7.9 occurrences.

Prediction 3: Initiation of socio-sexual behaviours will be frequent between different age categories to reduce tension.

The individuals in the group were reclassified into age categories adult, young adult, adolescent and juvenile. The relationship of socio-sexual behaviour between the age categories shows that the distribution across the age group is different and individuals are more likely to initiate and receive socio-sexual contact with individuals of differing age groups than with individuals in the same age group and the result is significant, (Chi Sq = 235.417, df = 4, and P = <0.001). The table below (3f) shows the frequencies and percentages for each age category.

Age group - Initiator / Age group - Receiver							
			Age group - receiver				Total
			Adult	Young adult	Juvenile	Adolescent	
Age group – initiator	Adult	Frequency	8	80	4	0	92
		Percentage	8.7%	87.0%	4.3%	0%	100.0%
	Young adult	Count	31	52	95	18	196
		% within Age group	15.8%	26.5%	48.5%	9.2%	100.0%
	Juvenile	Count	4	70	0	37	111
		% within Age group	3.6%	63.1%	0%	33.3%	100.0%
	Adolescent	Count	5	55	61	0	121
		% within Age group	4.1%	45.5%	50.4%	0%	100.0%
Total	Count	48	257	160	55	520	
	% within Age group	9.2%	49.4%	30.8%	10.6%	100.0%	

Table 3.j. Age groups of initiator and receiver and the frequency/percentage of socio-sexual behaviours.

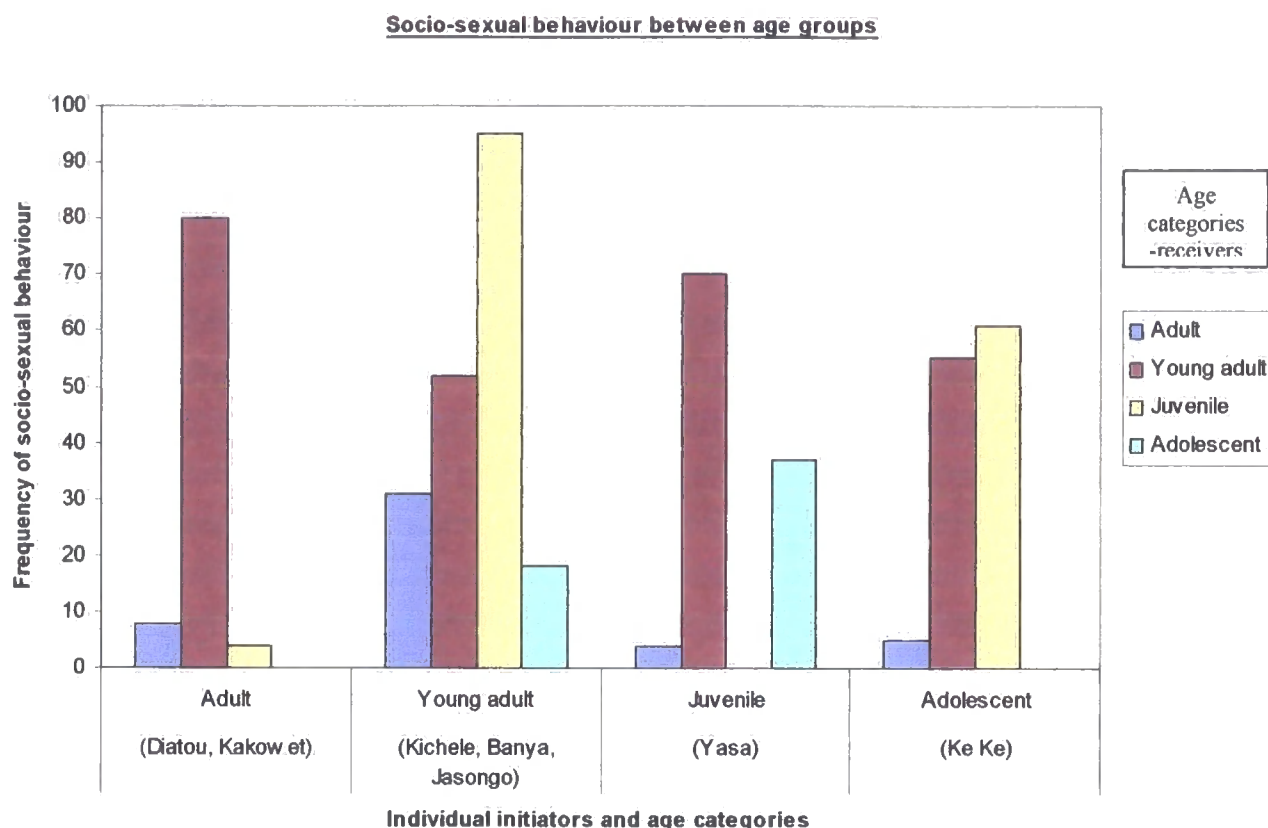


Figure 3.2k Socio-sexual behaviour between age categories (adult, young adult, Juvenile and adolescent). Each category is shown as initiator and receiver

The above chart (Fig 3.2k) shows that the juvenile and adolescent categories only have one individual in each, Yasa and Ke Ke respectively and as such juvenile/juvenile and adolescent/adolescent categories are blank.

The table shows that adults initiate socio-sexual behaviour with other adults infrequently, only 8.7% of the total time, compared to the other age groups and for the juvenile the same was true. Only two individuals, one of each sex, composed this group and this is probably reflected in the relatively low frequency. No adults initiated with the adolescent at all, but this can probably be explained by the fact that the two adults Diatou and Kakowet II are the parents of the adolescent Ke Ke. By far the most frequent socio-sexual partners were the young adults with 87% of all occurrences. This category as well as

containing sexually mature individuals also contained the only non-related individual (to all other group members) Banya and Jasongo who was distantly related to Diatou (studbook).

Socio-sexual initiation by the young adults with adults was low at 15.8% of all young adult initiations. The same is true with the adolescent Ke Ke at 9.2% and of the three young adults only Banya initiated with Ke Ke. Kichele was his half sister and Jasongo, a male (male/male socio-sexual contact was very infrequent). Socio-sexual contact between the young adults was higher at 26.5% and all individuals were of a similar age 11/12 years and non-related. The highest frequency of socio-sexual contact, almost half at 48.5%, was with the juvenile female Yasa, possibly because Yasa was a frequent partner in play, often leading to socio-sexual contact, especially between Kichele and Yasa who are half sisters.

For the juvenile female Yasa, initiation of socio-sexual contact was very low with adults, only 3.6% of all her initiations, which was to be expected with both adults being her parents. Socio-sexual initiation with Ke Ke, Yasa's brother was relatively high at 33.3% and frequently in a play context. Ke Ke and Yasa, the youngest individuals, spent a great deal of time playing and socio-sexual behaviour was included in this play. Although the juvenile's most frequent socio-sexual partners were the young adults at 63.1%, possibly because they are the largest group. Although this category also includes two young females, one Yasa's half sister Kichele, whom Yasa would frequently engage with in socio-sexual behaviour.

The adolescent male Ke Ke initiated with the adults very infrequently; only 4.1% of all his initiations and for the same reasons as Yasa, both are his parents. Initiation with the young adults is high, almost half at 45.5% and with the juvenile Yasa slightly higher at 50.4%. Yasa was the most frequent socio-sexual partner/category probably due to her age and being close kin, but also probably due to play and that she is the only female that he can dominate. Within the young adults, Banya was the most frequent individual Ke Ke initiated with for sex; she is the only unrelated female to Ke Ke in the group.

In summary the results supported the prediction, although with a limited number of individuals in each category, other factors including kin relations may affect the results.

Prediction 4: Socio-sexual behaviours will be frequent between same sex individuals (non-fertile pairs)

For statistical analysis each socio-sexual occurrence between two individuals was reclassified into sex categories; whether this involved both males, both females or was mixed sex. There were a total of 523 occurrences of sexual behaviour, with 3 occurrences between males, 255 occurrences between females and 265 occurrences between males and females. When the two categories male/male and female/female were compared the results showed a very clear pattern, male/male sexual contact was very infrequent and female/female sexual contact very frequent and the result is highly significant, (Chi Sq = 50.189, df = 1 and P = <0.001).

Sex of initiator / Sex of receiver					
			Sex of receiver		Total
			Female	Male	
Sex of initiator	Female	Count	255	100	355
		% within Sex/init	71.8%	28.2%	100.0%
	Male	Count	165	3	168
		% within Sex/init	98.2%	1.8%	100.0%
Total		Count	420	103	523
		% within Sex/init	80.3%	19.7%	100.0%

Table 3.k Socio-sexual behaviour between same sex individuals

Socio-sexual behaviours between females and between males

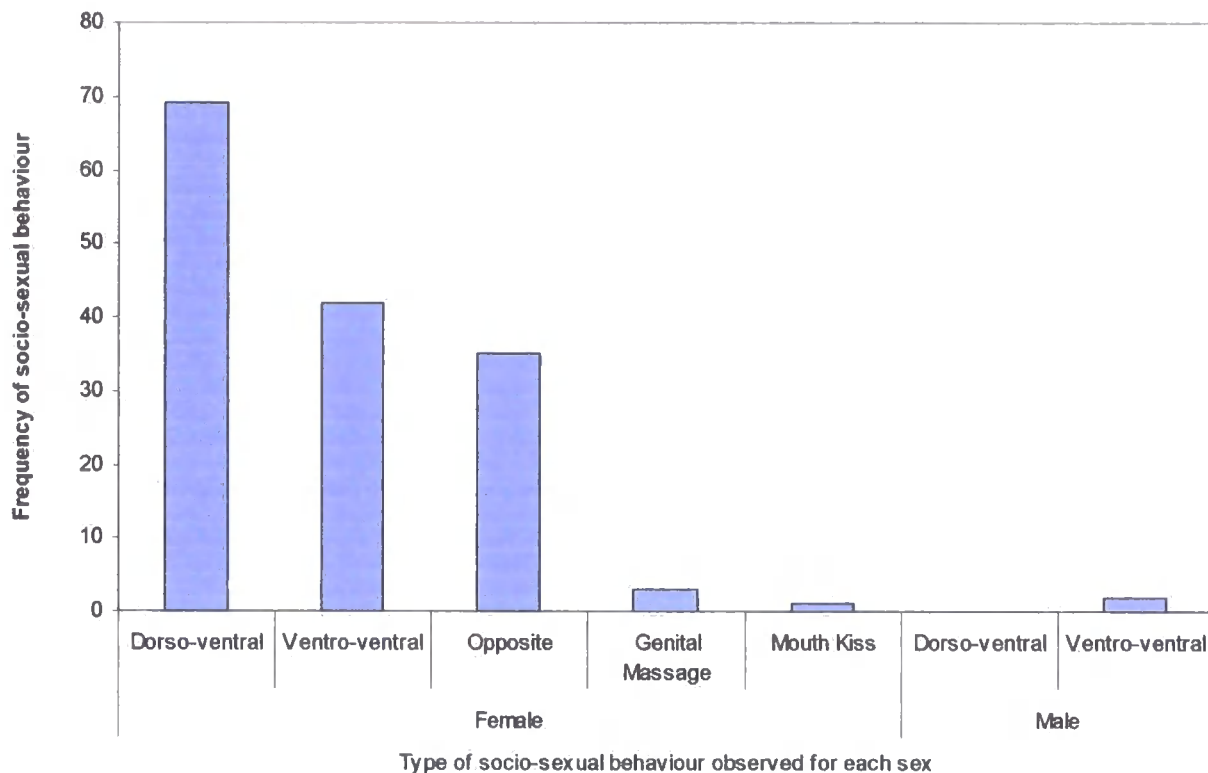


Figure 3.2m Socio-sexual behaviour between the sexes and the type of behaviour observed

Fig 3.2m shows clearly how infrequent male/male socio-sexual behaviour was in the group and of that only ventro-ventral was observed. In contrast female/female socio-sexual behaviour was very frequent and more diverse in type with occurrences of females genitally massaging another female and mouth kiss between them.

Overall females initiated 355 occurrences and received 420 occurrences of socio-sexual contact, far higher than males who initiated 168 occurrences and received 103 occurrences. It was found that overall males initiated with females as a socio-sexual partner 98.2% of the time and with other males only 1.8% of the time. Females initiated socio-sexual contact with other females 72% of the time, statistically slightly less than the expected 80.3%

and males 28% of the time, statistically slightly more than the expected 19.7%, based on the frequency of sexual occurrences.

Therefore the results support the prediction in relation to females but not male same sex socio-sexual contact, which was extremely low.

Prediction 5: Assuming dominance plays a role in tension regulation, dorso-ventral and ventro-ventral mounting would be expected to be more frequent than non-mounting socio-sexual behaviour.

For this analysis, socio-sexual behaviour types were reclassified into two categories (where possible) mounting (dorso-ventral and ventro-ventral) and non-mounting (opposite, genital massage, oral and mouth kiss). The frequency of each category was calculated and out of a total of 526 occurrences, 352 were found to be mounting socio-sexual behaviours and 174 were non-mounting socio-sexual behaviours. Mounting socio-sexual behaviours therefore were found to be more frequent than non-mounting socio-sexual behaviours and this is highly significant ($\chi^2 = 60.236$, $df = 1$, $P = <0.001$). Therefore the data support the prediction that mounting socio-sexual behaviours are more frequent than non-mounting.

When the age category of individuals and the initiator/receiver are included there is a difference between age categories for the initiator and receiver for mounting socio-sexual behaviours and the result is significant ($\chi^2 = 169.997$, $df = 9$, $P = <0.001$). For example young adults were receivers of a mounting socio-sexual behaviour on 77 occurrences when adults initiated, but young adults initiated with adults on only 23 occurrences. For non-mounting socio-sexual behaviours data were insufficient and the result was therefore inconclusive. For age categories therefore the results partly support the prediction, mounting socio-sexual behaviours between the age categories were more frequent than non-mounting.

The table (3h) below illustrates this. Figure 3.2n following the table provides a visual representation of the frequency of the socio-sexual behaviours in the two categories.

Initiators age/Receivers age - Mounting/non-mounting

Mounting/non mounting				Receivers age				Total
				Juvenile	Adult	Young adult	Adolescent	
Mounting	Initiators age	Juvenile	Count %	2 3.8%	3 5.8%	33 63.5%	14 26.9%	52 100.0%
		Adult	Count %	4 4.6%	6 6.9%	77 88.5%	0 0%	87 100.0%
		Young adult	Count %	65 49.2%	23 17.4%	37 28.0%	7 5.3%	132 100.0%
		Adolescent	Count %	49 60.5%	0 0%	32 39.5%	0 0%	81 100.0%
		Total	Count %	120 34.1%	32 9.1%	179 50.9%	21 6.0%	352 100.0%
Non mounting	Initiators age	Juvenile	Count %	0 0%	1 1.6%	37 60.7%	23 37.7%	61 100.0%
		Adult	Count %	0 0%	2 33.3%	4 66.7%	0 0%	6 100.0%
		Young adult	Count %	31 48.4%	8 12.5%	15 23.4%	10 15.6%	64 100.0%
		Adolescent	Count %	10 23.3%	5 11.6%	27 62.8%	1 2.3%	43 100.0%
		Total	Count %	41 23.6%	16 9.2%	83 47.7%	34 19.5%	174 100.0%

Table 3.m Socio-sexual behaviour categorised into mounting and non-mounting behaviour, combined with age categories of the initiator and receiver

Socio-sexual behaviours for all Individuals

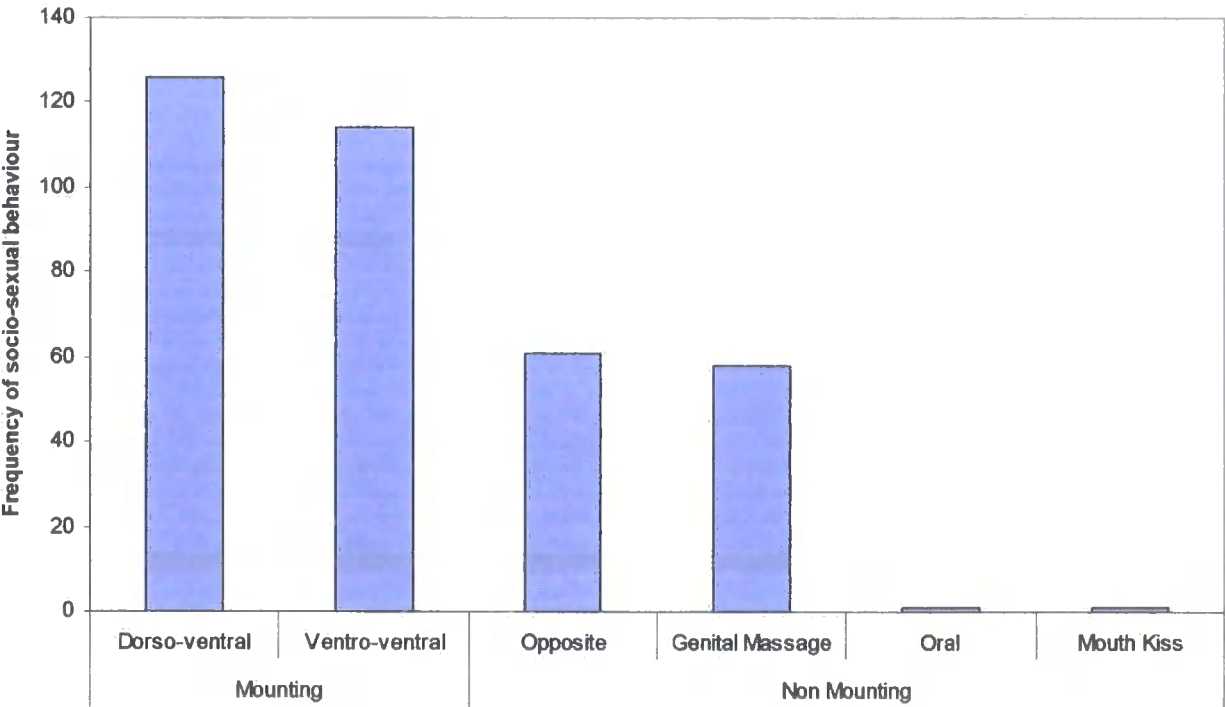


Figure 3.2n Types of socio-sexual behaviour (mounting and non-mounting) and frequency

Hypothesis 3 – Socio-sexual behaviours are an expression of Social Status Rank description

The data needed to test this hypothesis includes an analysis of the rank hierarchy. For the Twycross group social status or rank was deduced by the outcome of agonistic interactions and displacement data, as there were very few instances of competition over food between individuals in the group. An individual winning more often against another individual was considered to be dominant within the dyad and from this two categories of rank were produced.

Table (3.3i) on page 87 shows the agonistic interactions and displacement scores for all individuals in the Twycross group. The individual was taken to be dominant if the ratio was greater than 1.00 (e.g. 8.00 D>J, Diatou is dominant over Jasongo) and subordinate if less than 1.00 (e.g. 0.31 Ka<D, Kakowet II is subordinate to Diatou). The results show that there is a non-linear hierarchy in the Twycross group. Yasa, the juvenile female, was found to have too little data for her rank to be ascertained and she was excluded from all rank related analysis.

Diatou was clearly the most dominant individual and Jasongo the most subordinate. For some individuals like Ke Ke the picture was less clear. Scores were low overall, with few agonistic interactions between some individuals and some interactions having no data recorded at all. However, towards the end of data collection when Ke Ke began challenging his father Kakowet II for male dominance in the group and this rank change was well documented and based on a high number of interactions between these two individuals.

For the purpose of the analysis, based on the interactions, individuals were grouped into two classes of rank position, based on the result of agonistic and displacement scores (table 3.3i). High-ranking individuals (Diatou, Kichele and Kakowet II) and low ranking individuals (Banya, Ke Ke and Jasongo).

Agonistic interactions and displacement scores for the Twycross Group

Dyad	A	D	T	A giv	A re	D giv	D rec	T giv	T rec	Rank
D - Ki	0	4	4	0		4		4		D>Ki
D - Ke	0	5	5	0		5		5		D>Ke
D - Y	0	2	2	0		2		2		D>Y
D - Ka	10	6	16	0.5		2		3.2		D>Ka
D - B	0	8	8	0		8		8		D>B
D - J	5	3	8	5		3		8		B>J
Ki - D	0	0	0	0		0		0		Ki<D
Ke - D	0	0	0	0		0		0		Ke<D
Y - D	0	0	0	0		0		0		Y<D
Ka - D	2	3	5	0.2		0.5		0.31		Ka<D
B - D	0	0	0	0		0		0		B<D
J - D	0	0	0	0		0		0		J<D
Ki - Ke	4	2	6	4		0.33		1		Ki>Ke
Ki - Y	0	0	0	0		0		0		N/A
Ki - Ka	0	2	2	0		0.5		0.4		Ki<Ka
Ki - B	0	2	2	0		2		2		Ki>B
Ki - J	4	5	9	4		5		9		Ki>J
Ke - Ki	0	6	6	0		3		1		Ke>Ki
Y - Ki	0	0	0	0		0		0		N/A
Ka - Ki	1	4	5	1		2		2.5		Ka>Ki
B - Ki	0	0	0	0		0		0		B<Ki
J - Ki	0	0	0	0		0		0		J<Ki
Ke - Y	1	7	8	1		7		8		Ke>Y
Ke - Ka	0	7	7	0		0.7		0.47		Ke<Ka
Ke - B	5	20	25	0.17		1.82		0.63		Ke<B
Ke - J	0	4	4	0		1		1		Ke<J
Y - Ke	0	0	0	0		0		0		Y<Ke
Ka - Ke	5	10	15	5		0.5		2.14		Ka>Ke
B - Ke	29	11	40	5.8		0.55		1.6		B>Ke
J - Ke	0	4	4	0		1		1		J>Ke
Y - Ka	0	0	0	0		0		0		N/A
Y - B	0	1	1	0		0.5		0.25		Y<B
Y - J	0	0	0	0		0		0		Y<J
Ka - Y	0	0	0	0		0		0		N/A
B - Y	2	2	4	2		2		4		B>Y
J - Y	0	1	1	0		1		1		J>Y
Ka - B	4	7	11	4		7		11		Ka>B
Ka - J	2	6	8	2		6		8		Ka>J
B - Ka	0	0	0	0		0		0		B<Ka
J - Ka	0	0	0	0		0		0		J<Ka
B - J	0	4	4	0		4		4		B>J
J - B	0	0	0	0		0		0		J<B

Table 3.3i. Agonistic interactions and displacement scores for the Twycross Group. Each individual dyad shows the agonistic (A), displacement (D) interactions between them and the total (T) overall. From this results allowed the highest scoring individuals to be classes as High rank and low scoring low rank.

Prediction 1: Initiation of socio-sexual behaviour shows status-dependent asymmetries

There were a total of 236 occurrences of socio-sexual behaviour, with 119 of these initiated by low ranking individuals and 117 by high-ranking individuals (as classified in the previous paragraph). Table (3.3ii) above shows that low rank individuals initiated socio-sexual behaviour with other low rank individuals on 55 occurrences and with high rank individuals on 64 occurrences. High rank individuals initiated socio-sexual behaviour with low rank individuals on 103 occurrences and with other high rank individuals on only 14 occasions. For low rank initiators there is a slight preference for high rank socio-sexual partners, but for high rank initiators there is a very strong preference for low rank socio-sexual partners. This suggests that there is asymmetry in rank and the result is significant (Chi Sq = 46.620, df = 1, P = <0.001) see table 3.3ii below. Therefore the results support the prediction.

			Receiver's Rank		Total
			Low rank	High rank	
Initiator's Rank	Low rank	Count % within Initiator	55 46.2%	64 53.8%	119 100.0%
	High rank	Count % within Initiator	103 88.0%	14 12.0%	117 100.0%
Total		Count % within Initiator	158 66.9%	78 33.1%	236 100.0%

Table 3.3ii. Rank of Initiator and receiver. High ranked individuals mainly initiated with those of low rank. For low ranked individuals rank initiation preference was less apparent.

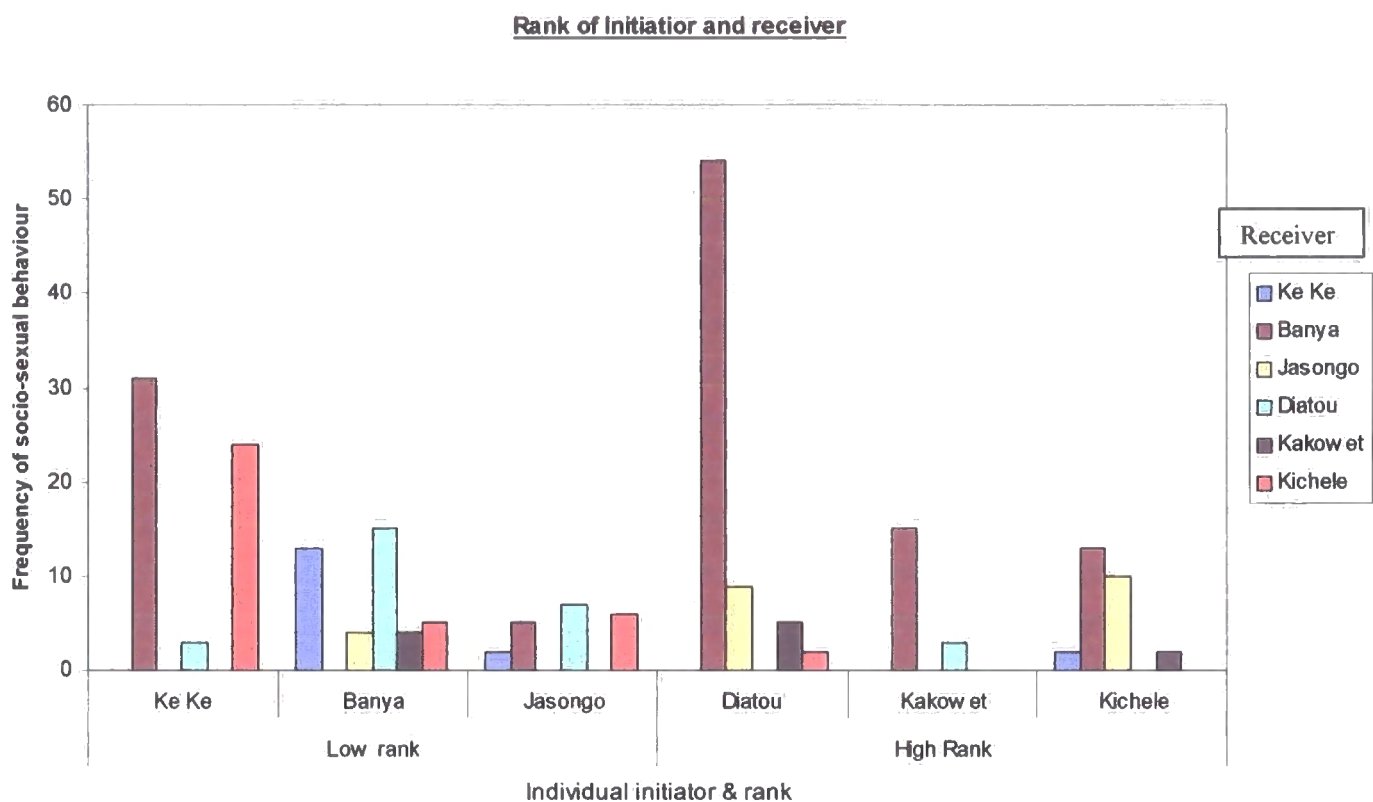


Fig (3.3a) The rank of Initiator and receiver. This is a breakdown of individuals in each rank and when each was the initiator and receiver in socio-sexual contact. This clearly shows individual differences, both in frequency and socio-sexual partner.

Fig (3.3a) above shows that for all three high ranked individuals low ranking Banya was the most frequent receiver, especially for Diatou, followed by Jasongo. For the low rank individuals rank preference is less defined, Ke Ke for example had preference for Banya and Kichele, both of differing ranks.

Prediction 2: Individual spatial position shows status-dependent asymmetries – whether individual is in the top or bottom position – horizontal only

A comparison between socio-sexual position (top/bottom) and rank was undertaken. The results for this prediction only includes data from mounting socio-sexual behaviours i.e. Vento-ventral and dorso-ventral, where this occurred in the horizontal position. The spatial position of individuals in non-mounting socio-sexual contact and mounting socio-sexual

behaviour, but not in a horizontal position, was unclear and these results were omitted from the analysis. For individuals in the top position in a socio-sexual behaviour, only those of high rank were the initiator, no individuals of low rank were observed to initiate in this top position. Therefore statistical analysis is not possible for the low rank category initiating in a top position. High ranked individuals in the top position initiated with low ranked individuals in the bottom position on 64 out of 68 occurrences, illustrating a very strong preference for differing rank and this is absent from table 3.3iii below.

For individuals who assumed the bottom position, statistical analysis was possible, although due to low cell counts this can only be really described because the expected value was smaller than 5, as required for the Chi-Sq test. Using the Fisher's Exact Test the result showed that there is a relationship between sexual position and rank ($P = <0.001$). Low ranking individuals who assumed the bottom position when initiating socio-sexual behaviour, always initiated with high-ranking individuals in 17/17 occurrences. High-ranking individuals on the bottom position who initiated socio-sexual behaviour always initiated with low ranking individuals on 4/4 occurrences. Therefore the data, although low overall, supports the prediction.

Socio-sexual position /Receiver position – Initiator's Rank / Receiver's Rank							
Receiver position	Sexual position				Receiver's Rank		Total
					Low rank	High rank	
Top	Bottom	Initiator's Rank	Low rank	Count	0	17	17
				% within Initiator	0%	100.0%	100.0%
		High rank	Count	4	0	4	
			% within Initiator	100.0%	0%	100.0%	
		Total		Count	4	17	21
		% within Initiator	19.0%	81.0%	100.0%		
Bottom	Top	Initiator's Rank	High rank	Count	64	1	65
				% within Initiator	98.5%	1.5%	100.0%
		Total		Count	64	1	65
		% within Initiator	98.5%	1.5%	100.0%		

Table 3.3iii. Socio-sexual position and rank. High ranked individuals were always in the top position and in all but one occurrence with a low ranking partner. No occurrences of low ranking individuals initiating in the bottom position were observed.

Prediction 3: High status/low status dyads have socio-sexual contact more frequently and for a longer duration than high status/high status or low status/low status dyads

For this analysis the rank of each individual, together with the frequency of socio-sexual behaviour and the duration, were analysed as follows.

Using the Oneway Anova test the result gives a significant anova ($F = 3.661$, $df\ 3/241$ $P = <0.014$). The variance is statistically homogenous, Levine's test = 0.067. As can be seen in table (3.3iv) below low status/low status dyads (5.20 seconds) are statistically different from high status/low status dyads (8.02 seconds). High status/high status dyads had the lowest value but because the sample size is small (17 occurrences) this gives a large standard error (1.00), therefore this is not statistically different to the other values.

The Scheffe test compares multiple pair-wise comparisons using post hoc tests. This was found to be statistically significant at the .05 level, individuals of differing ranks had socio-sexual contact for a longer duration than same ranked individuals. The longest duration of socio-sexual behaviour was between high status/low status dyads, a high ranking initiator and a low ranking receiver, with an average of 8.02 seconds, this combination was also the most frequent with 109 occurrences. A low ranking socio-sexual initiator and a high-ranking receiver had an average of 6.92 seconds and 64 occurrences. Low status/low status dyads had an average of 5.20 seconds and 55 occurrences and high status/high status dyads averaged 5.06 seconds with only 17 occurrences.

Comparison of Status and Duration						
	N	Mean	Std. Deviation	Std. Error	Minimum	Maximum
low-low	55	5.20	4.32	.58	1	24
Low-high	64	6.92	5.87	.73	1	27
high-low	109	8.02	6.31	.60	1	44
high-high	17	5.06	4.12	1.00	1	14
Total	245	6.89	5.76	.37	1	44

Table 3.3iv. Comparison of rank and duration of Socio-sexual behaviour. The highest duration of socio-sexual behaviours occurred with differing ranked partners. High rank initiating with low rank has the longest average duration, high rank with high rank the least duration.

The same rank mean is statistically lower than for the mixed rank mean, both same rank means are lower than opposite rank means. To test these rank pairs a standard T - test was carried out for the mixed group variable, a comparison of means. It was found that the distribution of same rank and mixed rank dyads was not equal (equal variances not assumed), (T Test $t = -3.572$, $df = 189.745$, $P = < 0.001$). The results found therefore support the prediction that socio-sexual behaviour is strongly influenced by social status.

Hypothesis 4: The function of socio-sexual behaviour is social bonding

Prediction 1: High frequency of socio-sexual behaviour between close spatial associates

Data required for this prediction included the frequency of each individual's socio-sexual partner correlated with the frequency of each individual's nearest neighbour (NN) or proximity scores. There was no correlation and therefore no statistical test could be undertaken. Each scatter plot shows the individual as the initiator if the first letter (i.e. D-J) or the receiver as the second letter (i.e. J-D) for socio-sexual behaviour. For the NN scores the second individual is the NN to the first individual, for example D-J, Jasongo is the NN for Diatou and J-D Diatou is the NN for Jasongo.

Diatou : Comparison of Nearest Neighbour and Sexual Behaviour

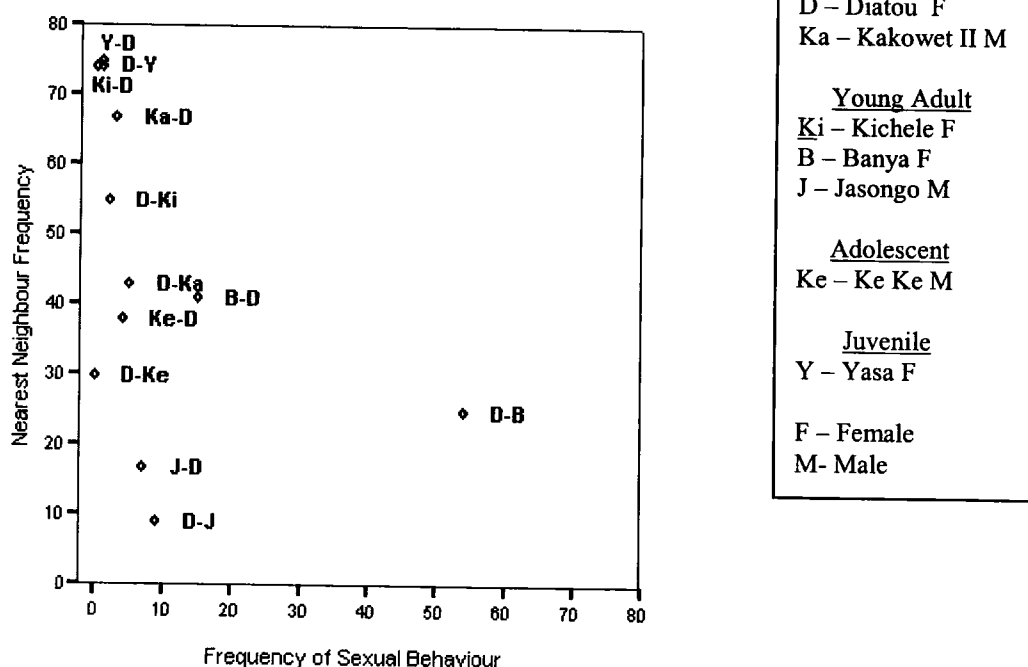


Figure 3.4a Frequency of each individual being Diatou's nearest neighbour and socio-sexual partner

For Diatou the dominant female (Fig 3.4a), it is clearly evident that the only frequent socio-sexual partner is Banya with 54 occurrences; the most frequent initiator was Diatou. Banya was infrequently Diatou's nearest neighbour in relation to the other individuals, although Diatou was more frequently Banya's nearest neighbour. The only other individual that was a less frequent nearest neighbour was Jasongo, the lowest ranking group member. Diatou's daughters Kichele, and Yasa had very infrequent socio-sexual contact with their mother, but were very frequent nearest neighbours for Diatou, as Diatou was to Kichele and Yasa. For Ke Ke, Diatou's son, he was an infrequent nearest neighbour for Diatou and had the lowest frequency of Diatou's siblings, both as a nearest neighbour and a socio-sexual partner. Therefore the results for Diatou do not support the prediction.

Kichele : Comparison of Nearest Neighbour and Sexual Behaviour

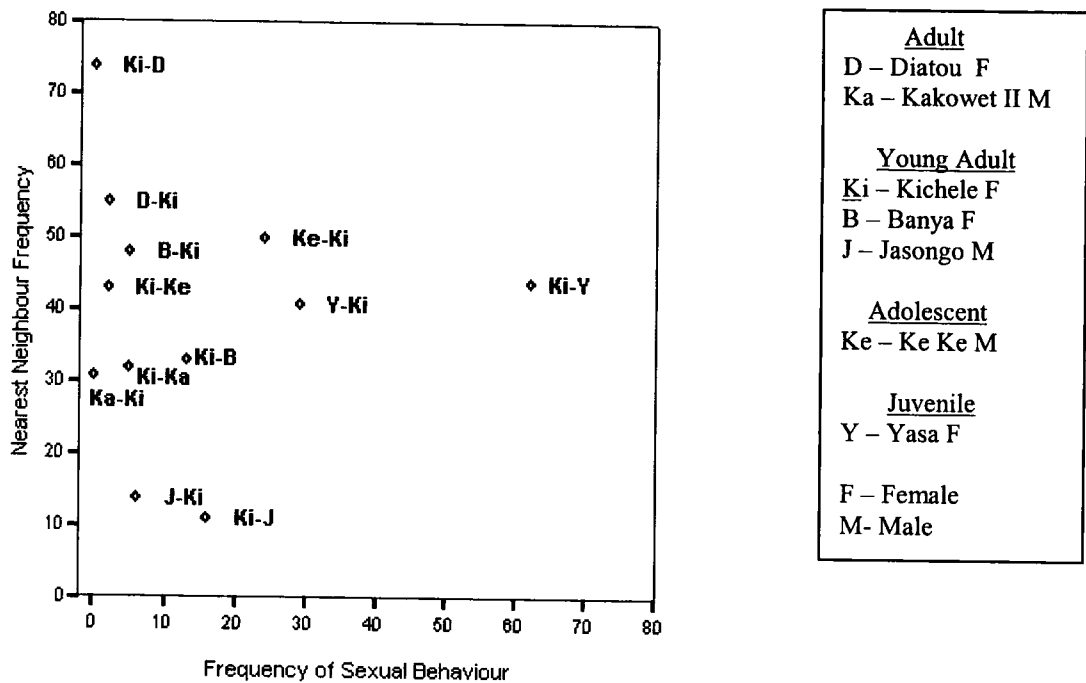


Figure 3.4b Frequency of each individual being Kichele's nearest neighbour and socio-sexual partner

Kichele shows a similar pattern to Diatou, with those individuals that are frequent nearest neighbours being infrequent socio-sexual partners. The exception to this is Yasa, Kichele's younger half sister, who was both a frequent nearest neighbour and by far the most frequent socio-sexual partner (initiated by Kichele). Although both are close kin, they are relatively young individuals, Kichele 12 years and Yasa 5 years, and socio-sexual behaviour was frequent in play. Ke Ke, Kichele's other sibling was also a frequent nearest neighbours to Kichele and relatively frequent socio-sexual partner, although initiation was by Ke Ke and not Kichele. Jasongo was the least frequent nearest neighbour and socio-sexual partner, although Kichele initiated socio-sexual behaviour with Jasongo more than Jasongo initiated with Kichele. The results for Kichele do not support the prediction

Ke Ke : Comparison of Nearest Neighbour and Sexual Behaviour

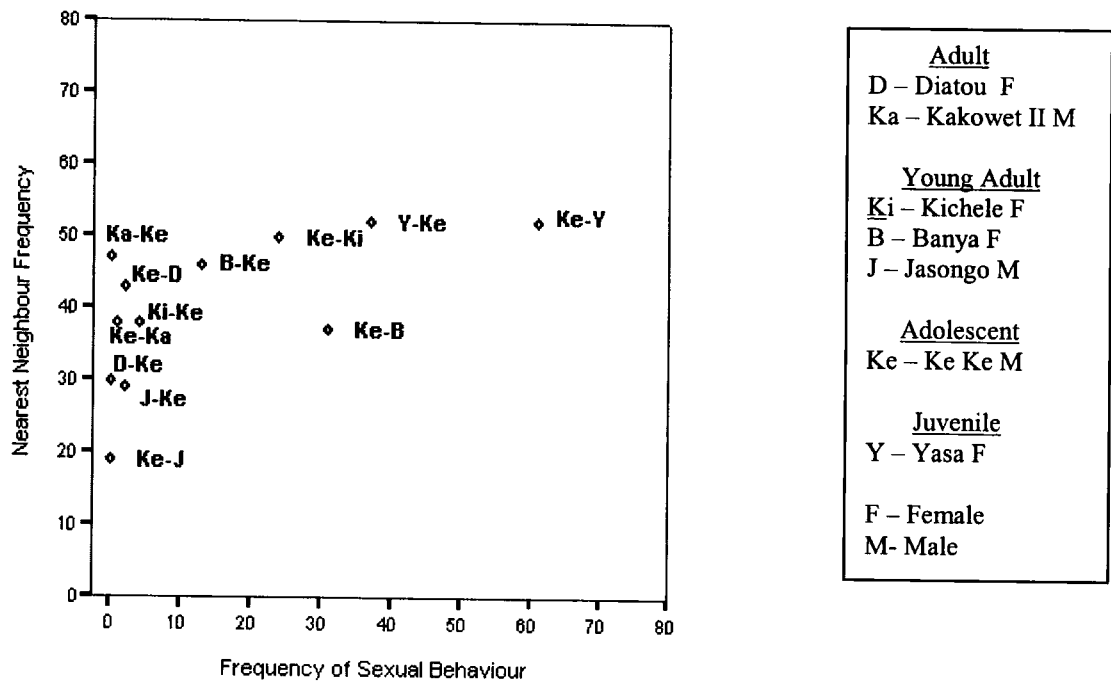


Figure 3.4c Frequency of each individual being Ke Ke's nearest neighbour and socio-sexual partner

For Ke Ke, the pattern is less clearly defined, but very little socio-sexual contact occurred with his mother Diatou and father Kakowet II and also the young adult male Jasongo. As with Kichele, Yasa is also by far the most frequent socio-sexual partner. Although full brother and sister, Ke Ke and Yasa are 8 and 5 years respectively, socio-sexual behaviour occurred frequently in a play context. Ke Ke initiated socio-sexual contact more than Yasa. The same pattern occurred with Banya, the next most frequent socio-sexual partner, but Banya initiated socio-sexual contact less frequently than Ke Ke. Ke Ke initiated socio-sexual behaviour most frequently with Banya, not surprising because Banya was a young low ranking adult female (12 years) and the only unrelated female in the group. The results generally do not support the prediction, apart from Yasa, who is a frequent socio-sexual partner and nearest neighbour.

Yasa : Comparison of Nearest Neighbour and Sexual Behaviour

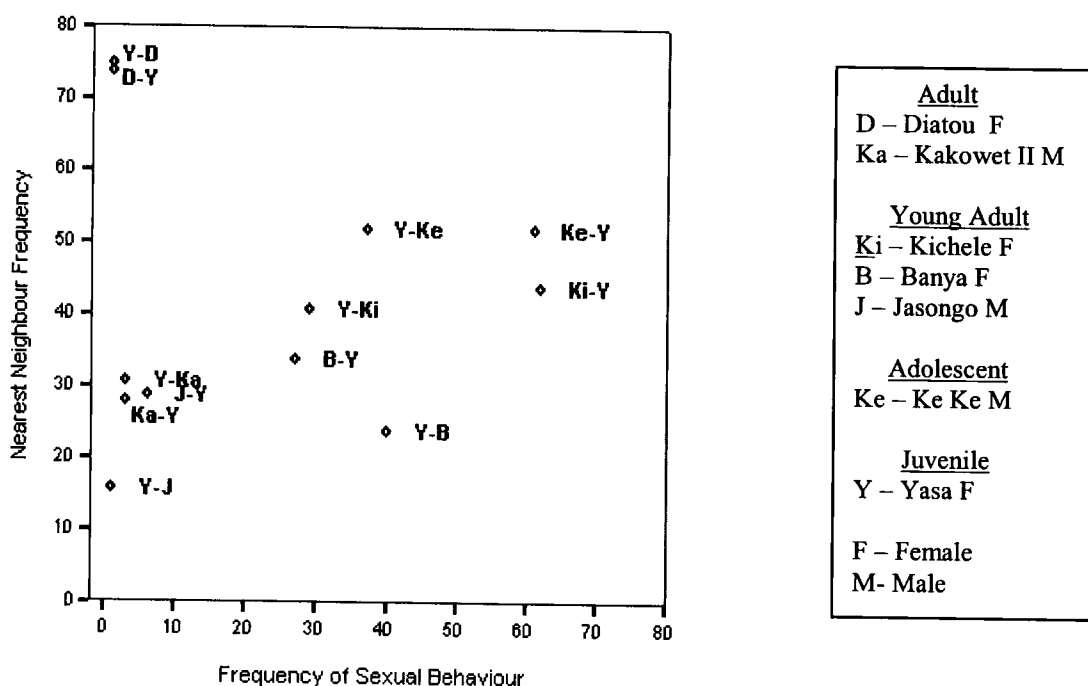


Figure 3.4d Frequency of each individual being Yasa's nearest neighbour and socio-sexual partner

For Yasa the most frequent nearest neighbour was her mother Diatou, which was expected. Yasa was the youngest individual and spent a lot of time with her mother Diatou. Yasa had almost no socio-sexual behaviour with Diatou or her father Kakowet II. Her brother Ke Ke and half-sister Kichele, were both frequent nearest neighbours and socio-sexual partners, probably because all were young individuals and close kin, and as such were frequently observed together. Kichele and Ke Ke initiated socio-sexual contact with Yasa far more than she did with them. Banya was also a frequent socio-sexual partner, but a less frequent nearest neighbour, and it is interesting to see that Banya was the only individual Yasa initiated socio-sexual behaviour with more than received. Banya was a relatively young female and unrelated to Yasa and as such maybe 'preferred' as a socio-sexual partner. The results for Yasa are mixed, only for Ke Ke and Kichele do the results support the prediction. The results for all other individuals do not support the prediction.

Kakowet : Comparison of Nearest Neighbour and Sexual Behaviour

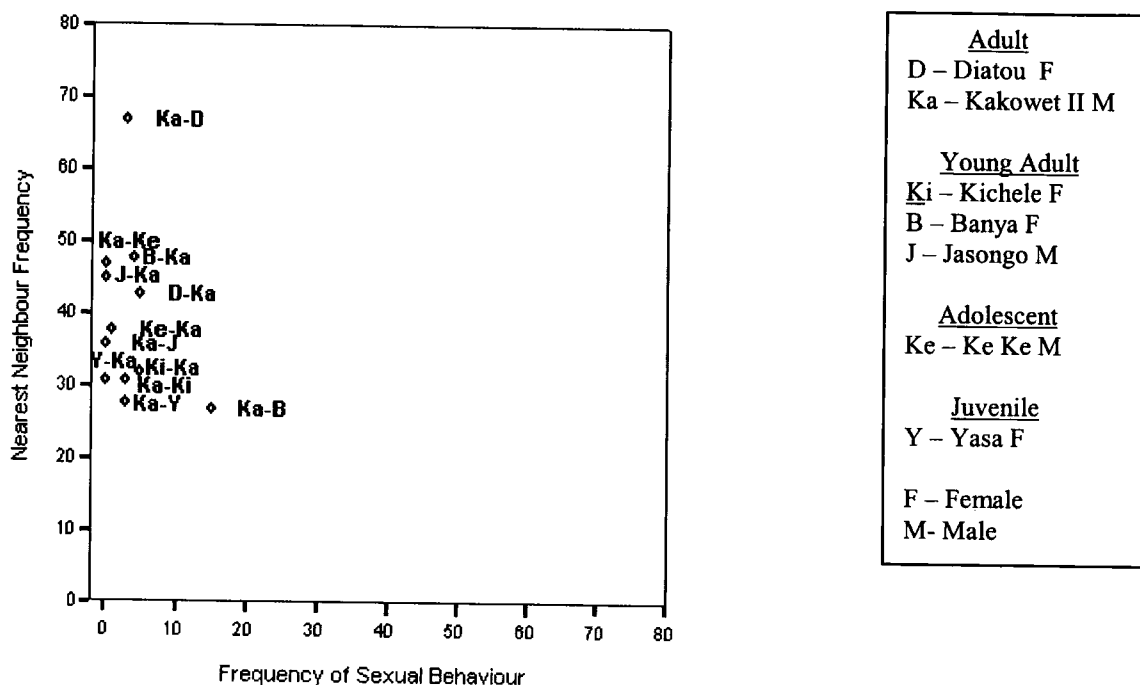


Figure 3.4e Frequency of each individual being Kakowet's nearest neighbour and socio-sexual partner

The frequency of socio-sexual behaviour for Kakowet II was very limited; he was one of the least sexually active individuals in the group, along with Jasongo. There was little to differentiate between individuals regarding the frequency of nearest neighbour to Kakowet II apart from Diatou being the most frequent, followed by the two younger males Ke Ke and Jasongo. His most frequent socio-sexual partner and initiated by Kakowet II, was Banya the young adult female and the lowest in rank. The results for Kakowet II do not support the prediction.

Banya : Comparison of Nearest Neighbour and Sexual Behaviour

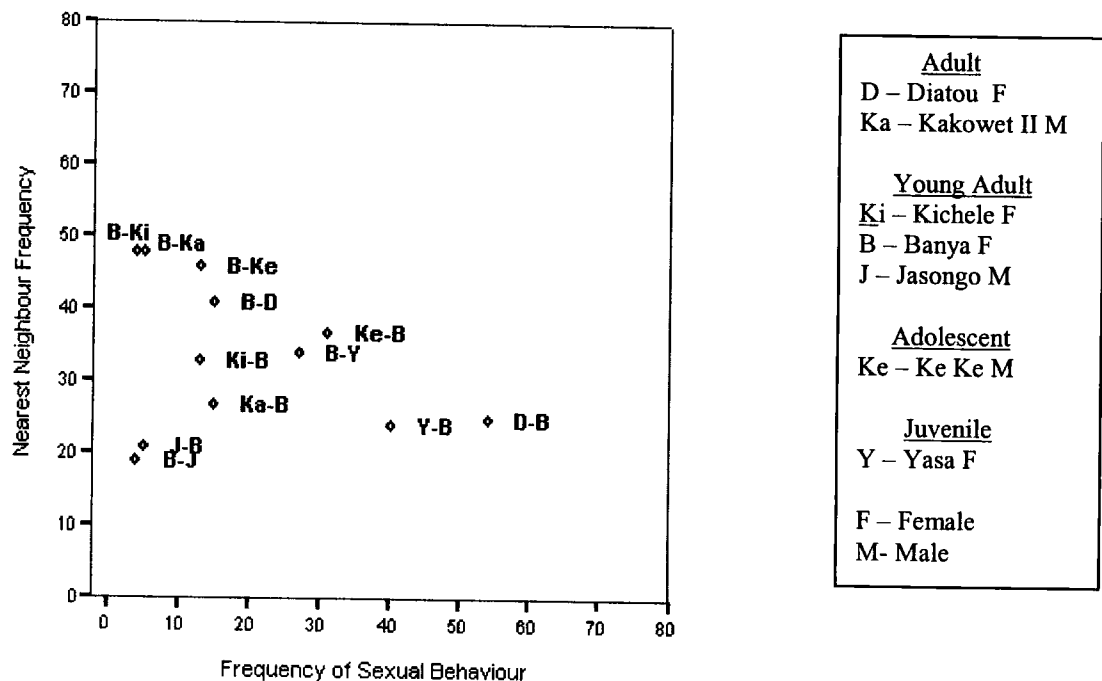


Figure 3.4f Frequency of each individual being Banya's nearest neighbour and socio-sexual partner

For Banya the frequency of nearest neighbour was limited to a smaller range, with Ke Ke, Kichele and Kakowet II being very similar and the most frequent nearest neighbours. Jasongo was the least frequent socio-sexual partner and nearest neighbour. The most frequent socio-sexual partners, Diatou and Yasa, were also similar in frequency but relatively infrequent nearest neighbours. These two females regularly initiated socio-sexual contact with Banya, rather than Banya making the initiation. Yasa was the one individual in the group that Banya initiated relatively frequent socio-sexual contact with. The results for Banya therefore do not support the prediction.

For Jasongo the frequency of nearest neighbour and socio-sexual partner was also limited, very similar to that of Kakowet II. The only distinctive nearest neighbour was Kakowet II, almost double the frequency of the next individual Ke Ke. No socio-sexual

behaviour was observed between Jasongo and Kakowet II. Interestingly the least frequent nearest nearest neighbours, Diatou and her eldest daughter Kichele, were the most frequent socio-sexual partners and also the highest-ranking females. Jasongo was also unrelated to all members of the group. Therefore for Jasongo frequent nearest neighbours were infrequent socio-sexual partners and this does not support the prediction.

Jasongo : Comparison of Nearest Neighbour and Sexual Behaviour

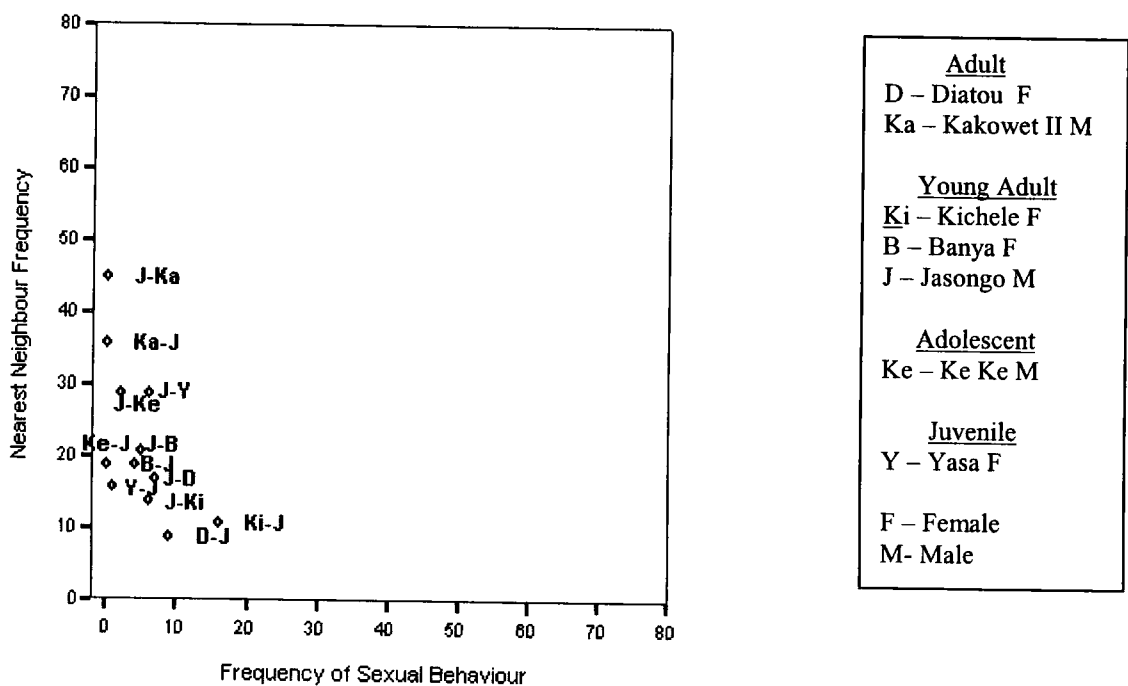


Figure 3.4g Frequency of each individual being Jasongo’s nearest neighbour and socio-sexual partner

Hypothesis 4 Prediction 2: Individuals who are frequent socio-sexual partners will also be frequent grooming partners.

As with the previous prediction, a bivariate correlation was completed and there was found to be no correlation. Scatter plots illustrate the relationship between the frequency of each individual being the socio-sexual partner and grooming partner of another. The positions

behaviour was observed between Jasongo and Kakowet II. Interestingly the least frequent nearest nearest neighbours, Diatou and her eldest daughter Kichele, were the most frequent socio-sexual partners and also the highest-ranking females. Jasongo was also unrelated to all members of the group. Therefore for Jasongo frequent nearest neighbours were infrequent socio-sexual partners and this does not support the prediction.

Jasongo : Comparison of Nearest Neighbour and Sexual Behaviour

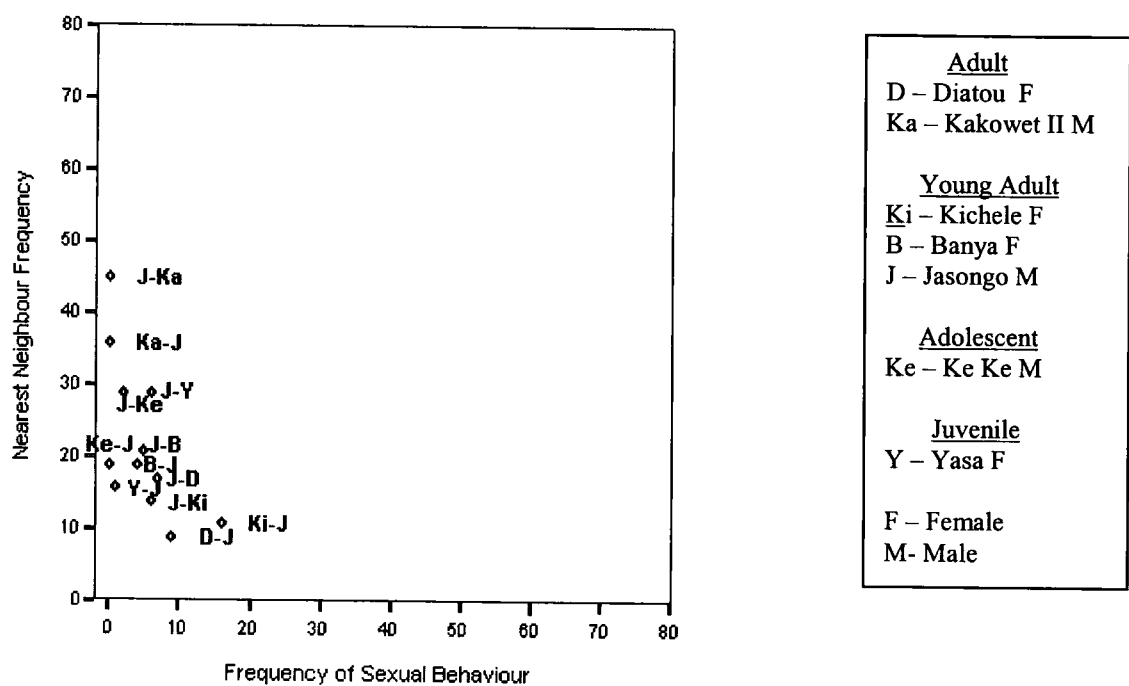


Figure 3.4g Frequency of each individual being Jasongo’s nearest neighbour and socio-sexual partner

Hypothesis 4 Prediction 2: Individuals who are frequent socio-sexual partners will also be frequent grooming partners.

As with the previous prediction, a bivariate correlation was completed and there was found to be no correlation. Scatter plots illustrate the relationship between the frequency of each individual being the socio-sexual partner and grooming partner of another. The positions

of initials in the following are not related to initiator and receiver and solely represent the frequency of occurrences between two individuals, hence there is only one pair combination.

Diatou : Comparison of Grooming and Sexual Behaviour

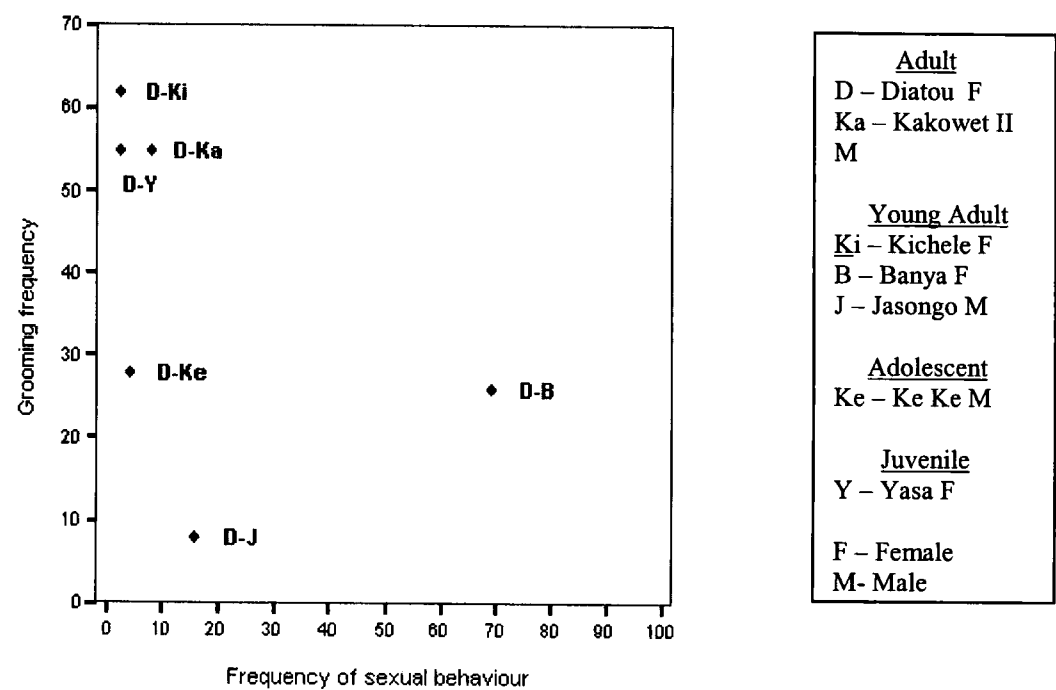


Figure 3.4h Frequency of each individual being Diatou’s grooming and socio-sexual partner

The first scatter plot (fig 3.4h) shows the relationship between the frequency of socio-sexual behaviour and grooming partner for Diatou. There is some kin/non-kin division around grooming, with Diatou grooming/being groomed by kin, her daughters Kichele and Yasa especially, but also the dominant male Kakowet II. All individuals have a low frequency of socio-sexual behaviour with Diatou except for Banya, who was almost exclusively Diatou’s main socio-sexual partner. Banya was however low down in grooming frequency, together with Jasongo and interestingly Banya is unrelated to Diatou, yet was the most frequent socio-sexual partner. The results for Diatou therefore do not support the prediction.



For Kichele (figure 3.4i) below the results are slightly different. There is one clear frequent socio-sexual (and to a lesser extent) grooming partner, Yasa. The most frequent grooming partner was her mother Diatou, although socio-sexual contact was almost non-existent. The remaining individuals are infrequent socio-sexual and grooming partners. Therefore for Kichele the results do support the prediction.

Kichele : Comparison of Grooming and Sexual Behaviour

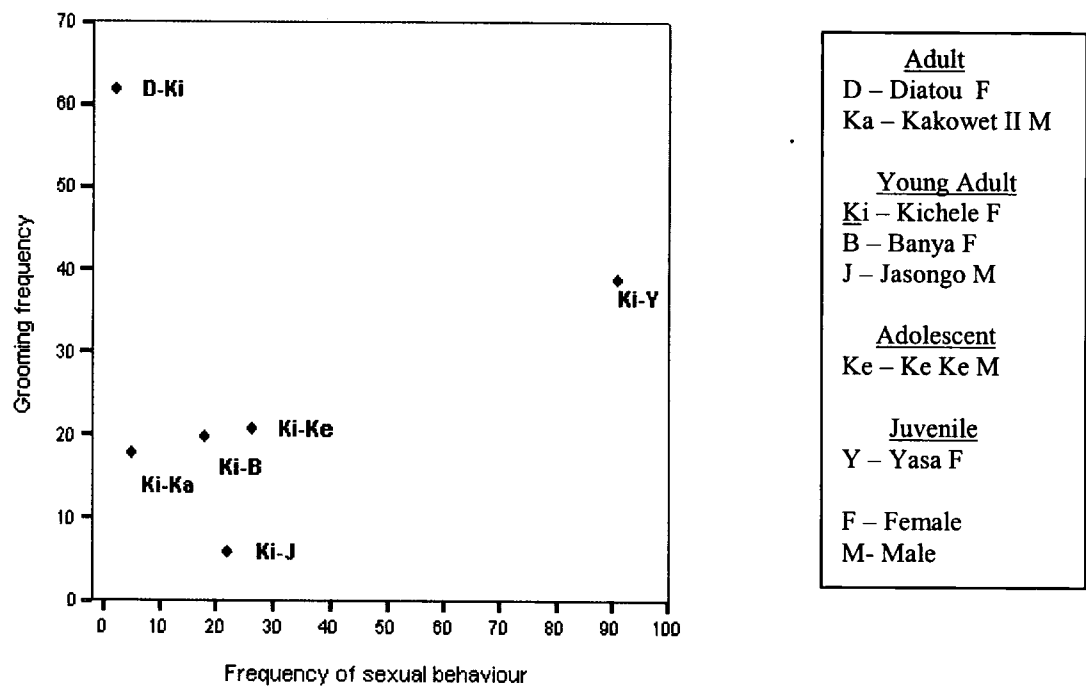


Figure 3.4i Frequency of each individual being Kichele’s grooming and socio-sexual partner

For Ke Ke (fig. 3.4j) a similar pattern occurs with regard to Yasa, she is also his younger sister and was by far the most frequent socio-sexual partner, but much less a grooming partner. For Ke Ke and Yasa, both young individuals, grooming tended to be lower in frequency and they were the groomee far more than the groomer. Interestingly the other two males in the group, Jasongo and Ke Ke’s father Kakowet II were very infrequent socio-

sexual or grooming partners. Female kin seem to be an important factor, with the top three most frequent grooming partners being his mother and two sisters. Banya was a frequent socio-sexual partner but a very infrequent grooming partner. Therefore the results do not support the prediction.

Ke Ke : Comparison of Grooming and Sexual Behaviour

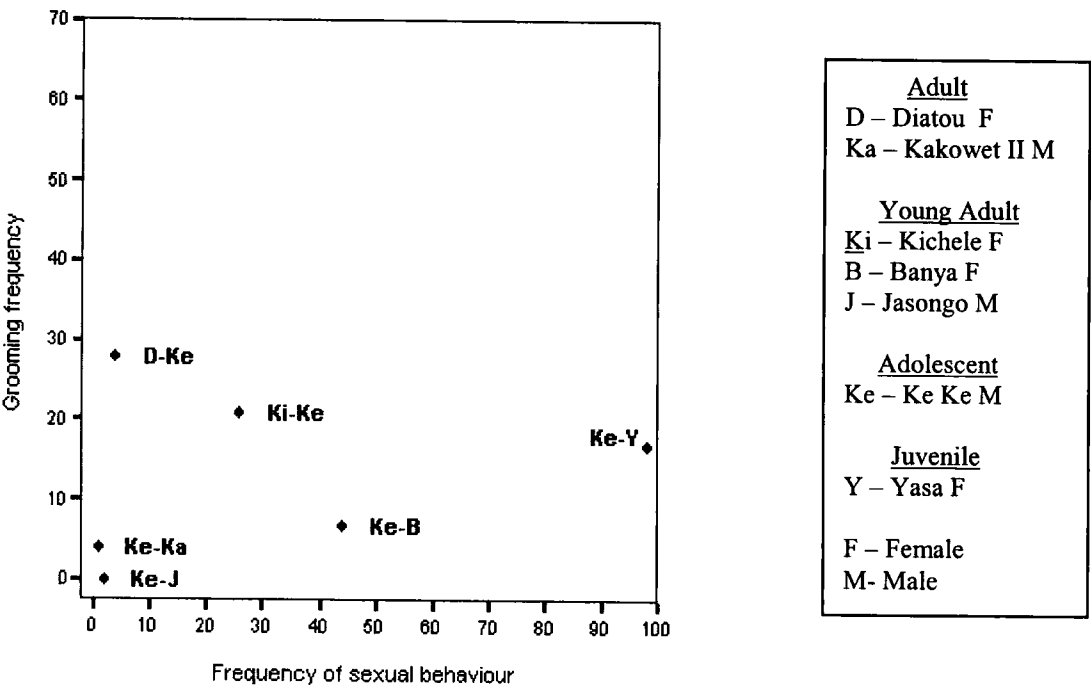


Figure 3.4j Frequency of each individual being Ke Ke’s grooming and socio-sexual partner

For Kakowet II (fig. 3.4k) all individuals apart from Diatou were infrequent socio-sexual and grooming partners. Diatou was by far the most frequent grooming partner as she was for most of the individuals in the group, although surprisingly Diatou was no more frequent than other individuals regarding socio-sexual behaviour, despite being the dominant

female. Overall for Kakowet II socio-sexual behaviour was very infrequent, which was surprising as he was the dominant male in the group. The results for Kakowet II do not support the prediction.

Kakowet II : Comparison of Grooming and Sexual Behaviour

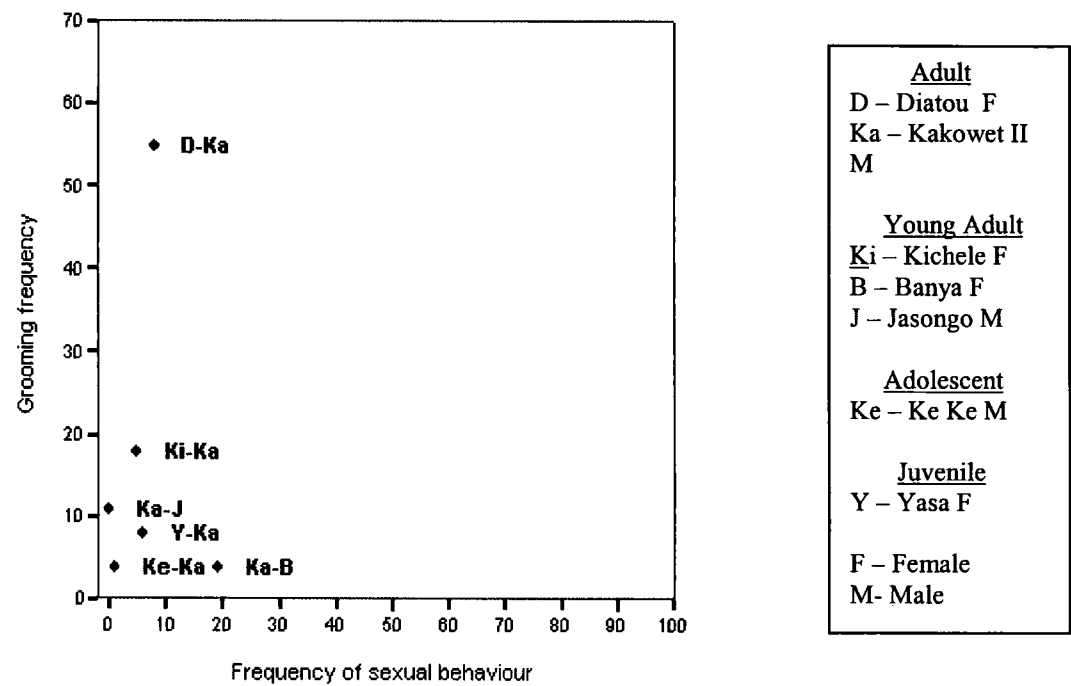


Figure 3.4k Frequency of each individual being Kakowet’s grooming and socio-sexual partner

Yasa : Comparison of Grooming and Sexual Behaviour

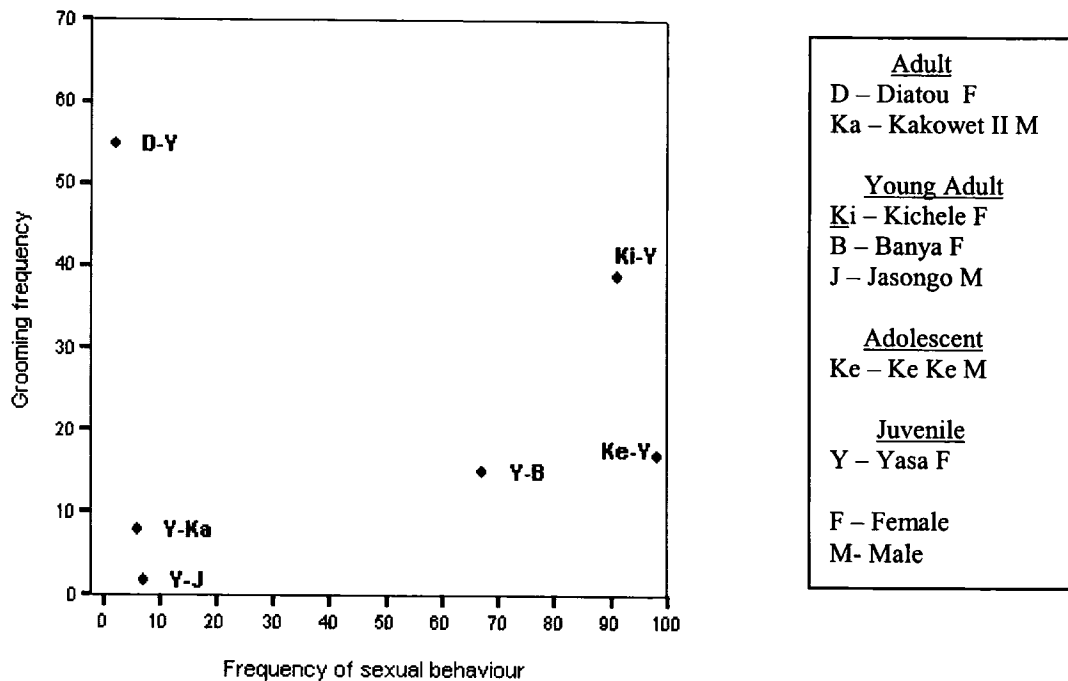


Figure 3.4m Frequency of each individual being Yasa's grooming and socio-sexual partner

For Yasa the pattern is not clearly defined. There was only one very frequent grooming partner, Diatou, her mother with whom socio-sexual contact was almost non-existent. With Ke Ke and Kichele, Yasa's siblings, socio-sexual contact was very frequent and with Kichele grooming was also frequent. Grooming between Yasa and Ke Ke was much less frequent and the focus between these individuals was play. Banya as a grooming partner was similar to Ke Ke although socio-sexual contact was relatively frequent, the highest for a non-related individual. Kakowet II, Yasa's father had little grooming or socio-sexual interaction with Yasa and along with Jasongo, had the least interaction with Yasa overall. Therefore the results for Yasa do not support the prediction.

For Banya grooming occurrences in particular were low in frequency compared to some other individuals. Banya was a low ranking female and the only unrelated female in the group. Diatou was the most frequent grooming and socio-sexual partner and this suggests a

positive relationship. Kichele on the other hand was a relatively frequent grooming partner, but relatively infrequent socio-sexual partner. Yasa is the opposite of Kichele, a very frequent socio-sexual partner but infrequent grooming partner. Jasongo and Kakowet II follow a similar pattern to other individuals, infrequent in interaction generally and especially socio-sexual behaviour and grooming. Ke Ke had a similar infrequent grooming pattern but was a frequent socio-sexual partner for Banya. Therefore for Banya there appears to be no relationship with grooming and socio-sexual behaviour and the prediction is not supported.

Banya : Comparison of Grooming and Sexual Behaviour

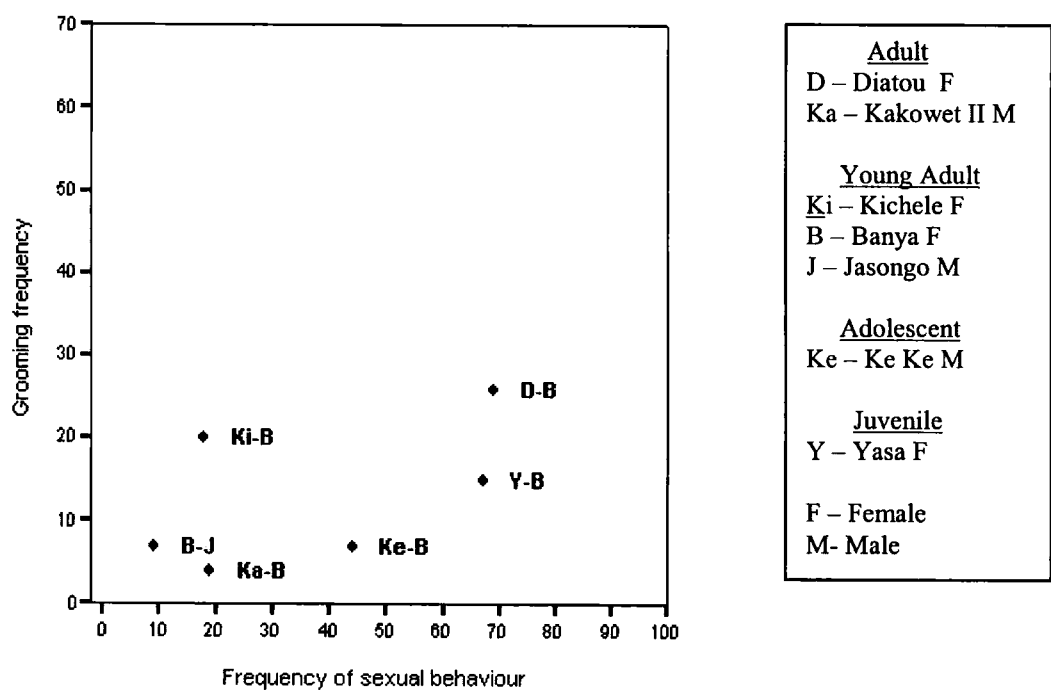


Figure 3.4n Frequency of each individual being Banya’s grooming and socio-sexual partner

Jasongo had the least interaction of any of the group members as can be seen in table (3.4o) with low interaction for both grooming and socio-sexual behaviour and all occurrences are clustered together. Jasongo was the lowest ranking individual and the only unrelated male

in the group. There is no relationship between grooming and socio-sexual partner. Jasongo and Kakowet II, the dominant male were the most frequent grooming partners, but even this was only 11 occurrences. The most socio-sexual contact was between Kichele and Diatou, the two most dominant females, but again this was very infrequent with a maximum of 22 occurrences with Kichele. For Jasongo data was limited and results do not support the prediction.

Jasongo : Comparison of Grooming and Sexual Behaviour

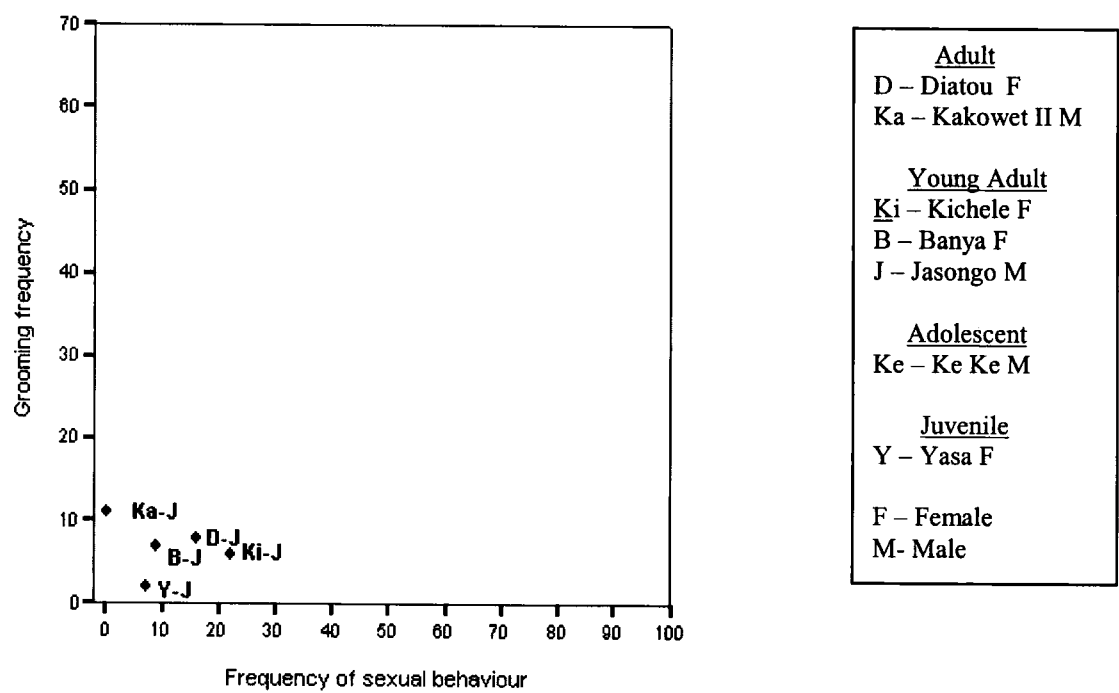


Figure 3.4o Frequency of each individual being Jasongo’s grooming and socio-sexual partner

Prediction 3: High frequency of socio-sexual contact among individuals of differing rank.

The following, (table 3.4i), shows the frequency and percentage of all socio-sexual behaviours according to rank. This shows that socio-sexual contact between individuals of differing rank is higher than between individuals of the same rank, (Chi Sq = 44.889, df = 1 and P = <0.001).

Initiators Rank / Receivers Rank					
			Receivers Rank		Total
			Low rank	High rank	
Initiators Rank	Low rank	Count	55	64	119
		% within Low Rank	46.2%	53.8%	100.0%
	High rank	Count	109	17	126
		% within High Rank	86.5%	13.5%	100.0%
Total	Count		164	81	245
	% within Initiator Rank		66.9%	33.1%	100.0%

Table 3.4i. The rank of initiator and receiver. High ranked individuals initiate most frequently with low ranked individuals, low ranked individuals initiate relatively equally with individuals in both rank categories.

Table 3.4i shows that overall 66.9 % of low ranked individuals were receivers in a socio-sexual contact and only 33.1% were of high rank. There are clearly far greater differences between different rank contacts than same rank contacts, therefore there is a relationship between rank and initiation and they are not independent of one another. High ranked individuals initiated with low ranked individuals in 86.5% of all occurrences and with other high ranked individuals only 13.5% of occurrences. Low ranked individuals initiated with low ranked individuals 46.2% of occurrences and with high ranked individuals 53.8% of occurrences. Therefore there is a preference for those of differing rank, but less so than for high ranked individuals. There are an equal number of both high and low ranked individuals (3) so bias has been minimised. One individual (Yasa) has been omitted from all rank data as she is a juvenile and the status is unclear. Status was deduced by aggression and displacement activity.

Prediction 4: That same sex socio-sexual behaviour would be frequent between females, who form the core of bonobo society and less frequent between males

If the male is the initiator then almost exclusively the receiver is female. For females there is a higher preference for males than by chance, although female/female sex is the most frequent and females are far more likely than males to be receivers. The results are largely due to the following socio-sexual partners, Kichele and Yasa who represent 36% of all female/female socio-sexual contacts, Diatou with Banya and Banya with Yasa, both with 27% of female/female contacts. Male/male socio-sexual contact was very infrequent with only 3 occurrences observed, which represents only 1.8% of all sexual contacts. Therefore same sex socio-sexual behaviour between females is much higher than between males, (Chi Sq = 50.189, df = 1, P = <0.001).

Sex of Initiator / Sex of Receiver					
			Sex of Receiver		Total
			Female	Male	
Sex of Initiator	Female	Count	255	100	355
		% within Female initiator	71.8%	28.2%	100.0%
	Male	Count	165	3	168
		% within Male initiator	98.2%	1.8%	100.0%
Total		Count	420	103	523
		% within Sex initiator	80.3%	19.7%	100.0%

Table 3.4ii. Sex of initiator and receiver. Female/female socio-sexual contact is the most frequent overall, male/male the least. Females initiate and receive the most SSB.

For this group only 36 ½ hours of data were collated and therefore statistical analysis for some predictions was not possible due to the lack of data. The following table (3.5i) shows the frequency, percentage and range of socio-sexual behaviours for the Planckendael group. The overall range of socio-sexual behaviours is similar to that found in the Twycross group but the frequencies of certain behaviours like self-genital massage are different. Self-genital massage was the most frequent socio-sexual behaviour with 56% of the total occurrences. This is far higher than for the Twycross group with 18% of the total occurrences and was largely due to the two juveniles present at Planckendael, especially the juvenile female Zomi. Dorso-ventral mounting and ventro-ventral mounting are the next most frequent at 18.9% and 17.7% respectively and were the most frequent socio-sexual behaviours for the adults in the group. Oral sex occurred more frequently in this group (7 occurrences) whereas this was only observed once in the Twycross group.

<u>Type</u>	<u>Frequency</u>	<u>Percentage</u>
Dorso-ventral	46	18.9
Ventro-ventral	43	17.7
Genital massage	4	1.6
Oral	7	2.9
Present	1	0.4
Mouth Kiss	4	1.6
Genital inspection	2	0.8
Self genital massage	136	56.0
Total	243	100

Table 3.5i All socio-sexual behaviours for the Planckendael group (percentage/frequency of each type)

Hypothesis 1: Reconciliation is in the form of socio-sexual behaviours

Agonistic interactions were very infrequent during the period of observation (although they had been frequent previously, with a change in group structure). Only 9 occurrences were observed and there were no particular individuals who were predominantly an aggressor or receiver. Therefore this hypothesis and associated predictions could not be tested.

Hypothesis 2: Socio-sexual behaviours are a form of tension regulation

Prediction 1: In feeding situations socio-sexual behaviours occur more often between owners of food and bystanders than between bystanders

Several feeding bouts were observed but socio-sexual behaviour was infrequent during such episodes and insufficient data were collated to enable analysis. Therefore this prediction could not be tested.

Prediction 2: The average duration of socio-sexual contacts would be expected to be higher during feeding, where tension is high, than in a non-feeding context

As with the previous prediction, socio-sexual behaviour during feeding bouts was limited and insufficient data were collated. Therefore this prediction could not be tested.

Prediction 3: Initiation of socio-sexual behaviours will be frequent between different age categories to reduce tension

The individuals in the group were reclassified into the same age categories as for the Twycross group adult, young adult, adolescent and juvenile. Young adult and adolescent categories have only one individual in each and as such the data are insufficient for statistical analysis (see table 3.5ii).

Age groups / Age group categories

			Age group categories				Total
			Adult	Young Adult	Adolescent	Juvenile	
Age groups	Adult	Count	10	0	0	11	21
		% within Age groups	47.6%	0%	0%	52.4%	100.0%
	Young Adult	Count	6	0	1	22	29
		% within Age groups	20.7%	0%	3.4%	75.9%	100.0%
	Adolescent	Count	13	0	0	3	16
		% within Age groups	81.3%	0%	0%	18.8%	100.0%
	Juvenile	Count	4	8	2	27	41
		% within Age groups	9.8%	19.5%	4.9%	65.9%	100.0%
Total	Count	33	8	3	63	107	
	% within Age groups	30.8%	7.5%	2.8%	58.9%	100.0%	

Table 3.5ii Socio-sexual behaviour between age categories. Only 1 young adult and adolescent were present in the group, hence no SSB between the same age category.

Although insufficient for statistical analysis, table 3.5ii illustrates the overall pattern of sexual behaviour within and between the various age categories for the Planckendael group. This shows that adults initiate with adults and juveniles, but not with the young adult or adolescent. These individuals are both males and the sons of one of the adult females, which may have influenced this.

The young adult male Redy initiated mostly with the juveniles and the young female Zomi in particular. Adults were the next most frequent category, although one of these was Redy's mother Hortense. The young adult initiated socio-sexual contact once with the adolescent Vifjio, his brother.

Vifjio initiated socio-sexual contact most frequently with the adults and to a lesser extent the juveniles. The juveniles were the most frequent sexual initiators for the group as a whole and most frequently with each other. The young adult Redy was the next most frequent receiver of the juveniles with adults and the adolescent infrequent receivers.

The categories of receivers were then further reduced into adult and juvenile because of insufficient data for adolescent and young adult categories, while leaving the initiator as the four original categories (see table 3.5iii)

Socio-sexual behaviour between age groups

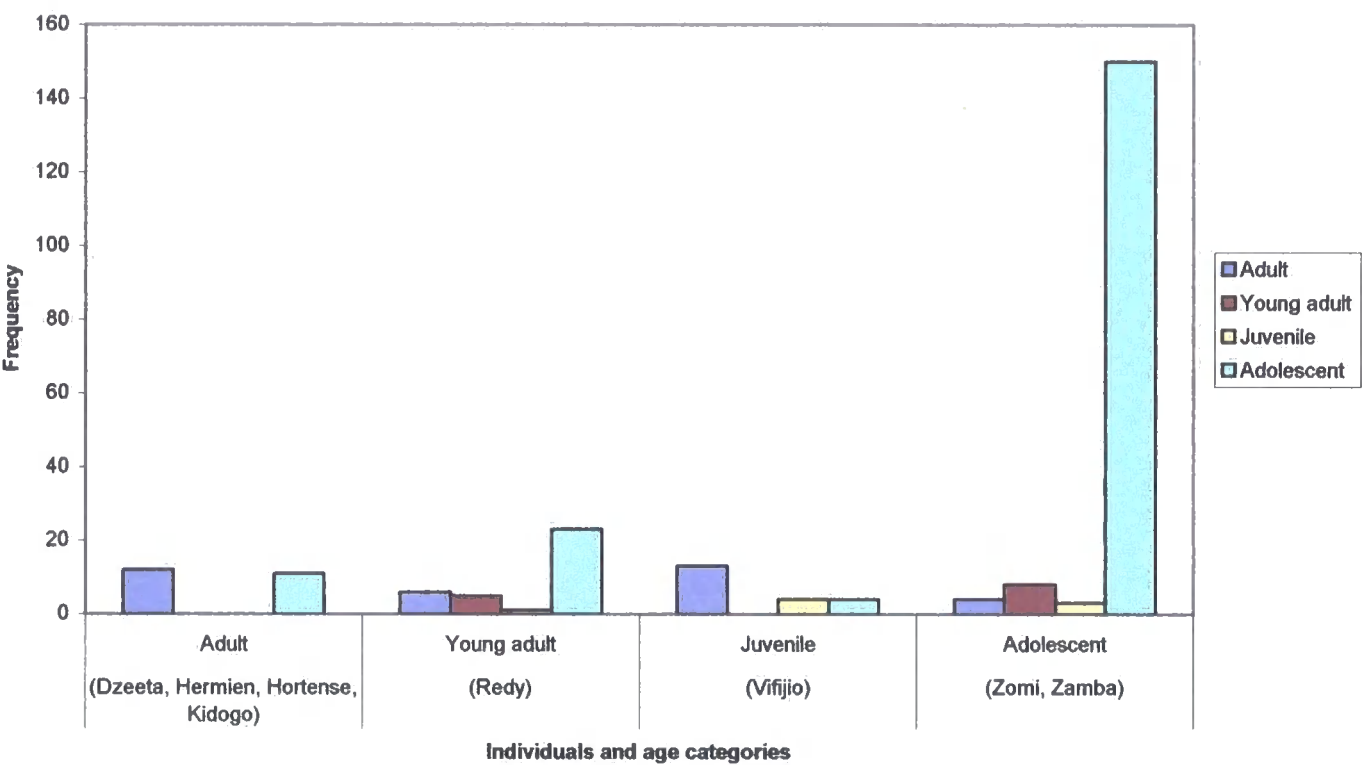


Figure 3.5a Socio-sexual behaviour between the age groups.

Age group of initiator / Age group of receiver					
			Age of receiver		Total
			Adult	Juvenile	
Age groups	Adult	Count	10	11	21
		% within Age groups	47.6%	52.4%	100.0%
	Young Adult	Count	6	22	28
		% within Age groups	21.4%	78.6%	100.0%
	Adolescent	Count	13	4	17
		% within Age groups	76.5%	23.5%	100.0%
	Juvenile	Count	4	26	30
		% within Age groups	13.3%	86.7%	100.0%
Total	Count	33	63	96	
	% within Age groups	34.4%	65.6%	100.0%	

Table 3.5iii Socio-sexual behaviour between age groups, initiator and receiver

The results show that there is a statistical difference with socio-sexual occurrence within or between the age categories ($\text{Chi Sq} = 22.955$, $\text{df} = 3$, $P = <0.001$), that the initiator is independent of the receiver. Table 3.5iii above shows the frequencies and percentages for each age category. The results for all individuals do not support the prediction, although when only selected age categories were selected (table 3.5iii) the results do support the prediction.

Prediction 4: Socio-sexual behaviours will be frequent between same sex individuals (non fertile pairs)

For statistical analysis the data was reclassified into sex categories, male and female. There were a total of 106 occurrences of socio-sexual behaviour, and when the two categories male/male and female/female were compared the results showed that male/male socio-sexual contact was less frequent than female/female sexual contact with 8 occurrences between males and 17 occurrences between females. Overall for both sexes, same sex socio-sexual contacts were less than expected, especially between the females, as this was high in the Twycross group. The greatest frequency was between males and females with 81 occurrences. Nevertheless the result is statistically significant ($\text{Chi Sq} = 26.764$, $\text{df} = 1$ and $P = <0.001$) and therefore the prediction is supported.

Socio-sexual behaviours between females and between males

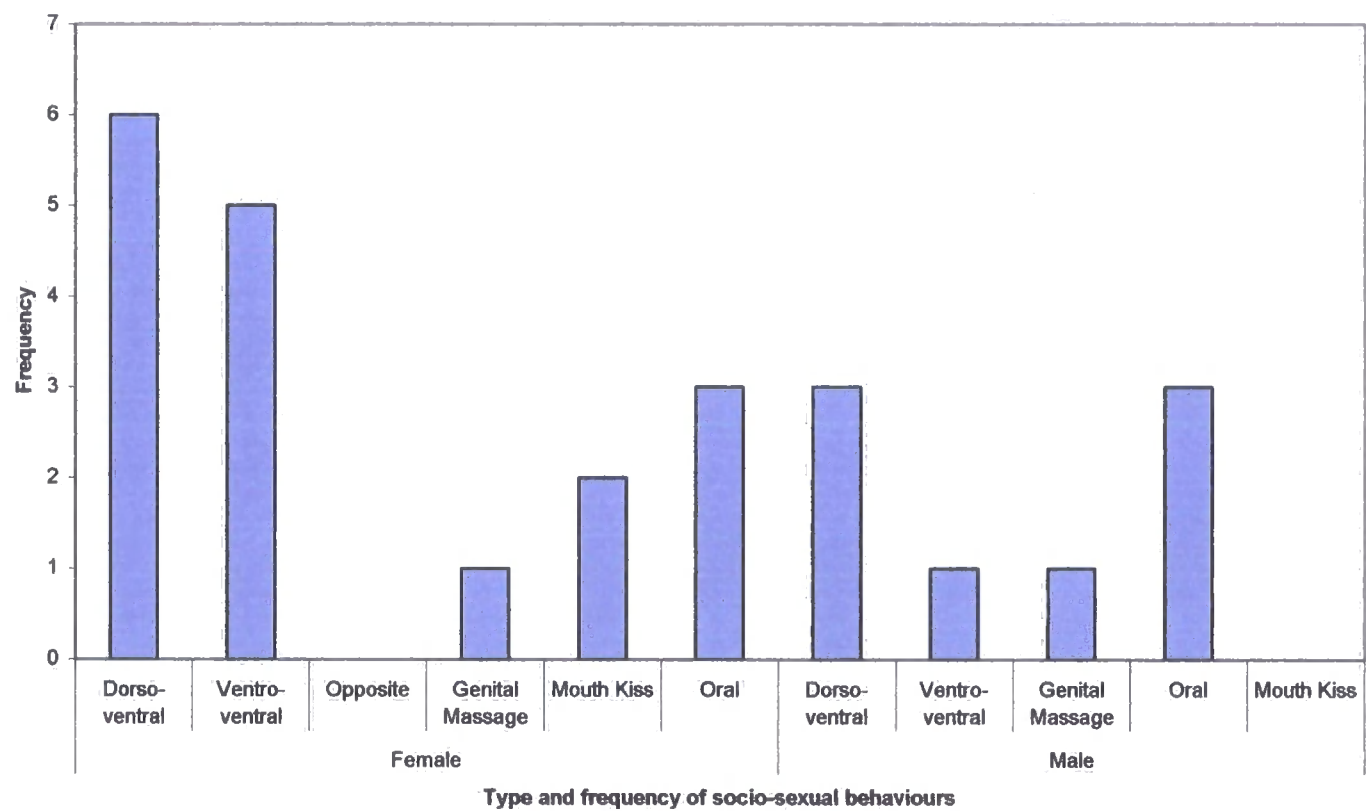


Figure 3.5b Types of socio-sexual behaviours and the frequency for males and females. Frequencies are low overall but especially for the males more diverse SSB than for the Twycross males.

Figure 3.5b shows that overall the Planckendael group have a greater range of socio-sexual behaviours observed between males and between females than the Twycross group. This is particularly evident between males where, although the frequency was low, this was due to a limited observation period rather than frequency. Oral sex and dorso-ventral were the most frequent between males, whereas between females dorso-ventral and ventro-ventral predominated, as it did in the Twycross group.

Male/female initiator / male/female receiver					
			Receiver		Total
			Male	Female	
Male/female initiator	Male	Count	8	55	63
		% within male/female initiator	12.7%	87.3%	100.0%
	Female	Count	26	17	43
		% within male/female initiator	60.5%	39.5%	100.0%
Total		Count	34	72	106
		% within male/female initiator	32.1%	67.9%	100.0%

Table 3.5iv Comparison of female/male as initiator and receiver

Overall males initiated more socio-sexual contact than females, and females received more socio-sexual contact than males. It was also found that overall males initiated with females as a socio-sexual partner 87.3% of all occurrences and with other males only 12.7% of occurrences, which is more than would be expected. Females initiated with other females 39.5% of occurrences, considerably less than expected and males 60.5% of occurrences, which is higher than expected.

When same sex socio-sexual contact is compared with mixed sex socio-sexual contact the results are also statistically significant (Chi Sq = 29.585, df = 1, P = <0.001) and the results also support the prediction.

Same sex / Mixed sex			
	Observed N	Expected N	Residual
Same sex	25	53.0	-28.0
Mixed	81	53.0	28.0
Total	106		

Table 3.5v Socio-sexual contact within and between the sexes.

Prediction 5: Assuming dominance plays a role in tension regulation, dorso-ventral and ventro-ventral mounting would be expected to be more frequent than non-mounting socio-sexual behaviour.

As with the data for the Twycross group, socio-sexual behaviours were reclassified into mounting and non-mounting sexual behaviour. The frequency of each was deduced and out of a total of 106 occurrences, 89 were mounting socio-sexual behaviours (dorso-ventral or

ventro-ventral) and 17 were non-mounting socio-sexual behaviours (all other types). The frequency of non-mounting/mounting socio-sexual behaviours is statistically unequal and mounting socio-sexual behaviours are more frequent than non-mounting socio-sexual

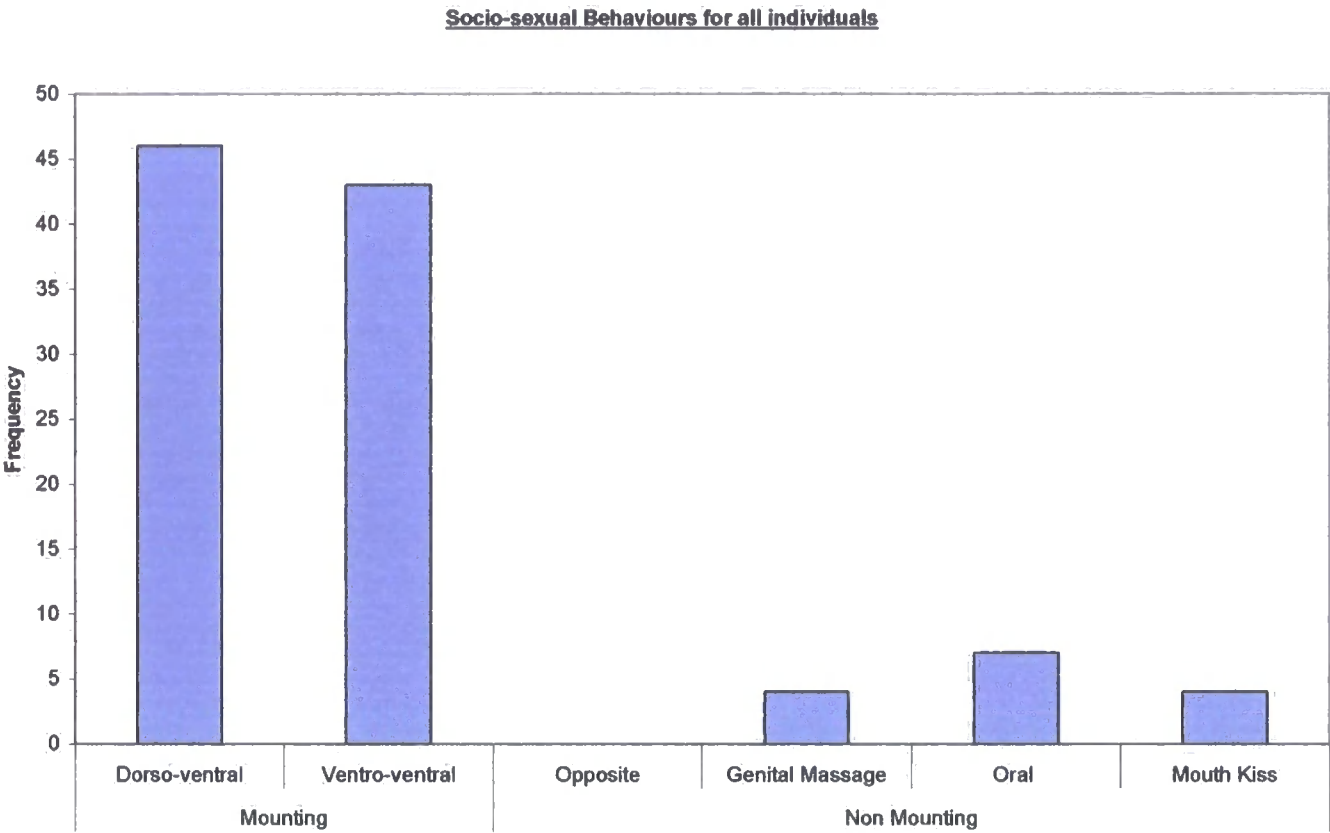


Figure 3.5c Frequency and type of socio-sexual behaviours, both mounting and non-mounting behaviours and the result is statistically significant (Chi Sq = 48.906, df = 1, P = <0.001) and supports the prediction.

Mounting / non mounting sexual behaviours					
		Frequency	Percent	Valid Percent	Cumulative Percent
Valid	Mounting	89	84.0	84.0	84.0
	Non Mounting	17	16.0	16.0	100.0
	Total	106	100.0	100.0	

Table 3.5vi Overall frequency and percentage of mounting and non-mounting socio-sexual behaviours

Hypothesis 3 – Socio-sexual behaviours are an expression of Social Status

For the Planckendael group the limited data produced insufficient agonistic interactions or displacement scores to deduce rank. The recent change in group dynamics and the limited time frame made this impossible to ascertain rank status. One individual Desmond, the dominant male had died in 2000 and two other females, Unga and Kozana had moved to other zoos one month prior to my visit (September 2001). Rank order for this group was given in Vervaecke et al (2000), although this was taken from data collected several years previously.

Hypothesis 4: Frequent sexual behaviour increases Social bonding

Prediction 1: High frequency of sexual behaviour between close spatial associates

For this prediction, the same procedure as for the Twycross group was followed; the frequency of each individual's socio-sexual partner was correlated with the frequency of each individual's nearest neighbour (NN), proximity score. There was no correlation and therefore no statistical test could be undertaken. Each scatter plot shows the individual as the initiator if the first letter (i.e. D-V) or the receiver as the second letter (i.e. V-D), for socio-sexual behaviour. For the NN scores the right hand individual (letter) is the NN to the left hand individual (letter), for example D-V, Vifjio is the NN for Dzeeta and V-D Dzeeta is the NN for Vifjio.

Dzeeta : Comparison of Nearest Neighbour and Sexual Behaviour

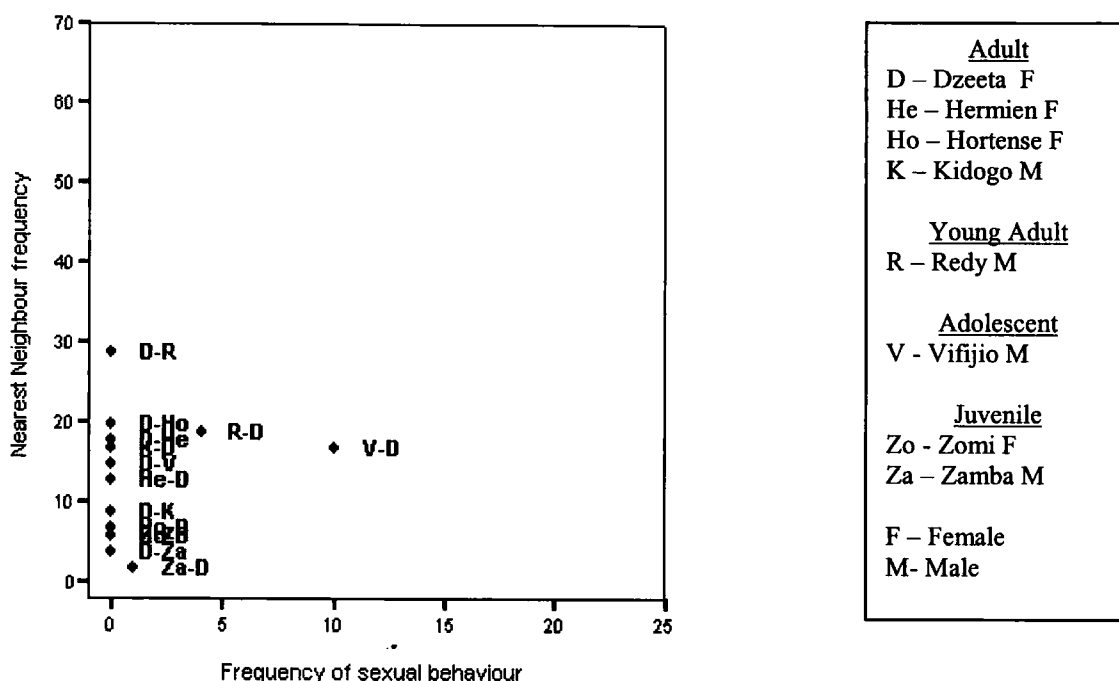


Figure 3.5d Frequency of each individual being Dzeeta's nearest neighbour and socio-sexual partner

For Dzeeta, possibly the dominant female (although due to a stroke she is now slow and interacts little with the other group members) socio-sexual contact is very infrequent with any individuals and none initiated by Dzeeta herself, only by Vifijio and Redy, Hortense's sons. These two individuals were also relatively frequent NN and for Dzeeta it appears that frequent NN are also frequent socio-sexual partners, although Dzeeta has no kin in the group and were this different then this would probably be reflected in the NN frequency. The two juveniles Zamba and Zomi were the least frequent on both NN and socio-sexual behaviour, which as they spend most of their time with their mothers was to be expected. Therefore for Dzeeta the results do not support the prediction.

Hermien : Comparison of Nearest Neighbour and Sexual Behaviour

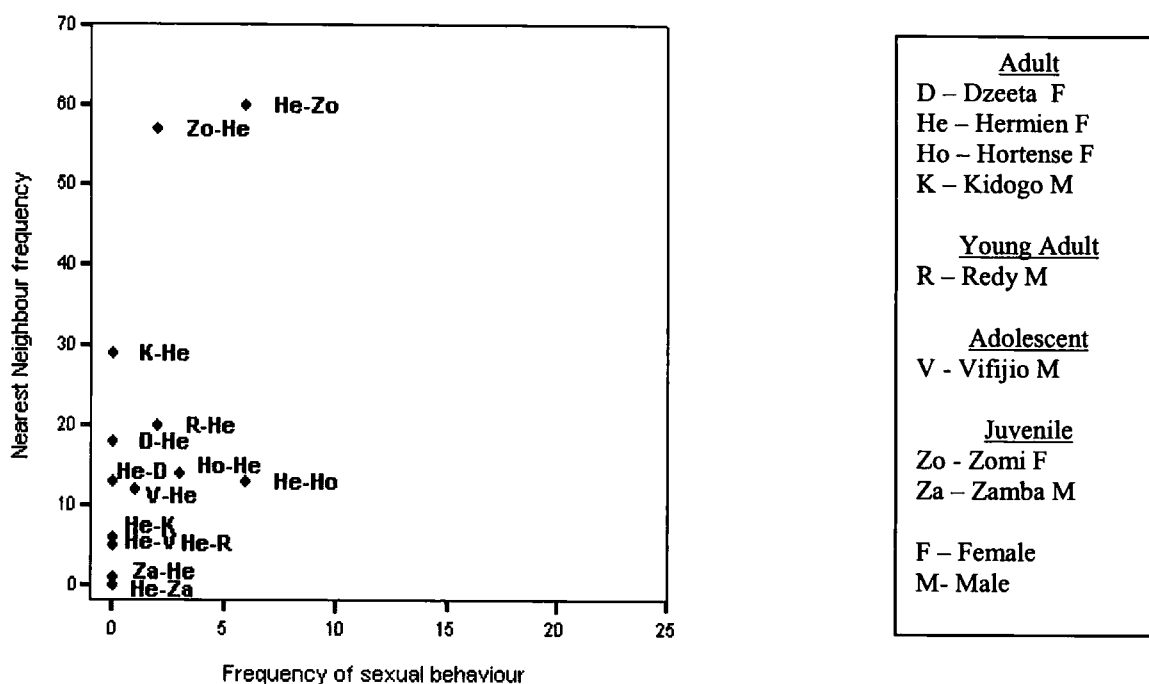


Figure 3.5e Frequency of each individual being Hermien's nearest neighbour and socio-sexual partner

Hermien's most frequent NN was not surprisingly Zomi her juvenile daughter and the frequency was far higher than for any other individual. Socio-sexual contact between mother and daughter did occur, always in a play context and mostly initiated by Hermien towards Zomi. The most frequent socio-sexual partner was Hortense, an adult female, most frequently initiated by Hermien. Both individuals were infrequent NN's to each other and no more than any other individual in the group. The individual Hermien had the least socio-sexual and NN contact with was Zamba, Hortense's juvenile son. The two adult males Redy and Kidogo were also infrequent NN and socio-sexual partners. The results for Hermien do not support the prediction.

For Hortense, the third adult female the NN frequency/socio-sexual behaviour frequency closely follows that of Hermien. Hortense also has a juvenile (Zamba) of the same

age as Zomi and as such Zamba and Hortense spend a considerable amount of time together. Socio-sexual behaviour initiated by Hortense occurred, also in a play context, but also one occurrence in a feeding context.

Hortense : Comparison of Nearest Neighbour and Sexual Behaviour

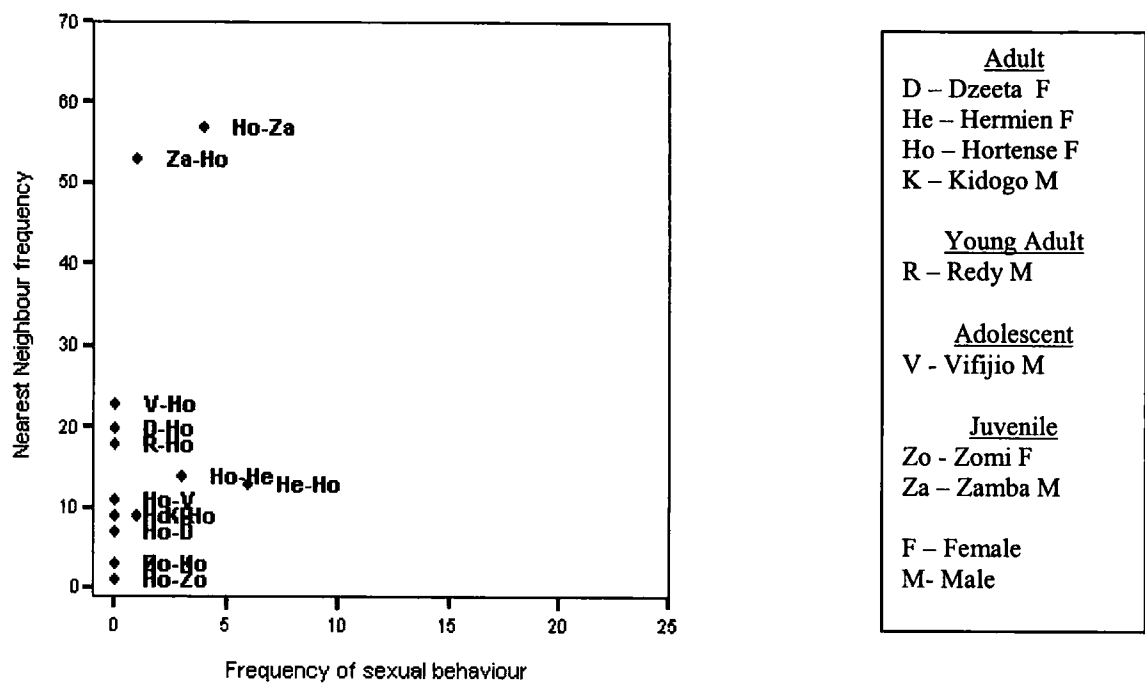


Figure 3.5f Frequency of each individual being Hortense’s nearest neighbour and socio-sexual partner

The only relatively frequent socio-sexual behaviour occurred with Hermien, with Hortense having no socio-sexual contact with other individuals. Hermien’s daughter Zomi was the least frequent NN and socio-sexual partner. Therefore as with Hermien, there is no relationship between NN frequency and socio-sexual behaviour frequency and the results do not support the prediction.

Redy is the youngest of two adult males and the son of Hortense and elder brother to Vifjio and Zamba. Although the youngest adult male Redy has a relatively large kin network and became the dominant male after the death of his father Desmond (also the dominant male). The most frequent socio-sexual contact is not with any of the adult females, but with

Zomi, Hermien’s daughter and most frequently initiated by Redy. Zomi was an infrequent NN to Redy and vice versa. Redy’s most frequent NN’s are the three adult females (including his mother Hortense) and his brother Vifijio. Although with all these individuals socio-sexual contact was very infrequent and the results do not support the prediction.

Redy : Comparison of Nearest Neighbour and Sexual Behaviour

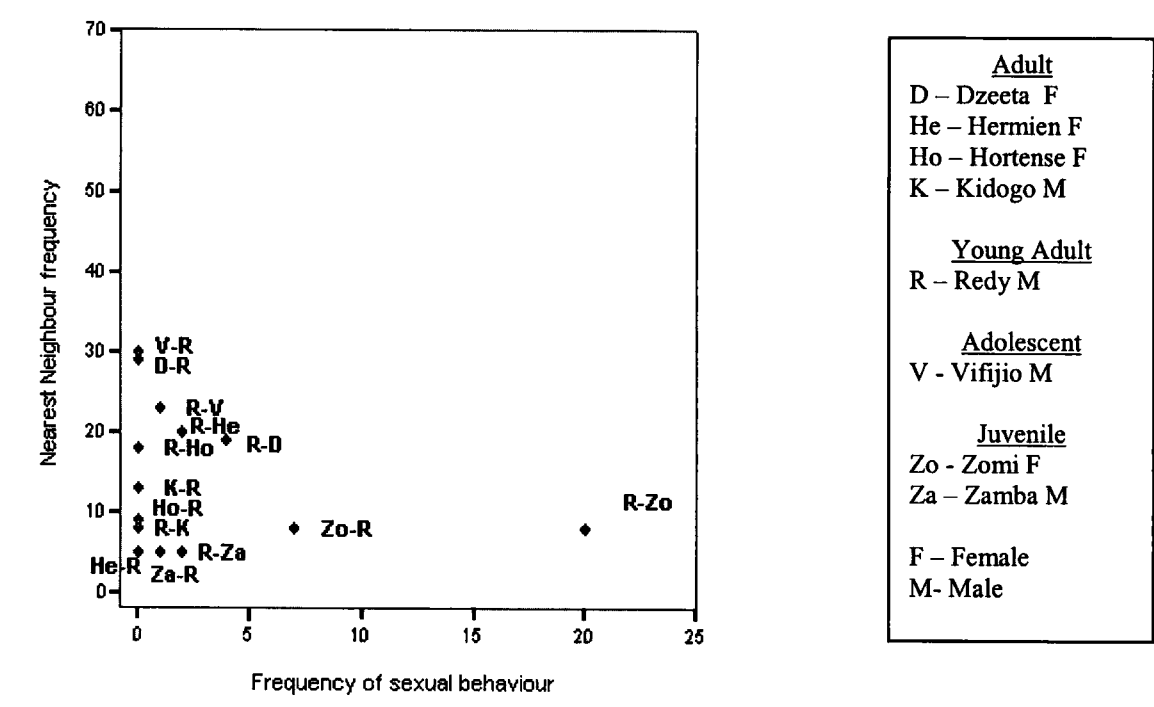


Figure 3.5g Frequency of each individual being Redy’s nearest neighbour and socio-sexual partner

Kidogo : Comparison of Nearest Neighbour and Sexual Behaviour

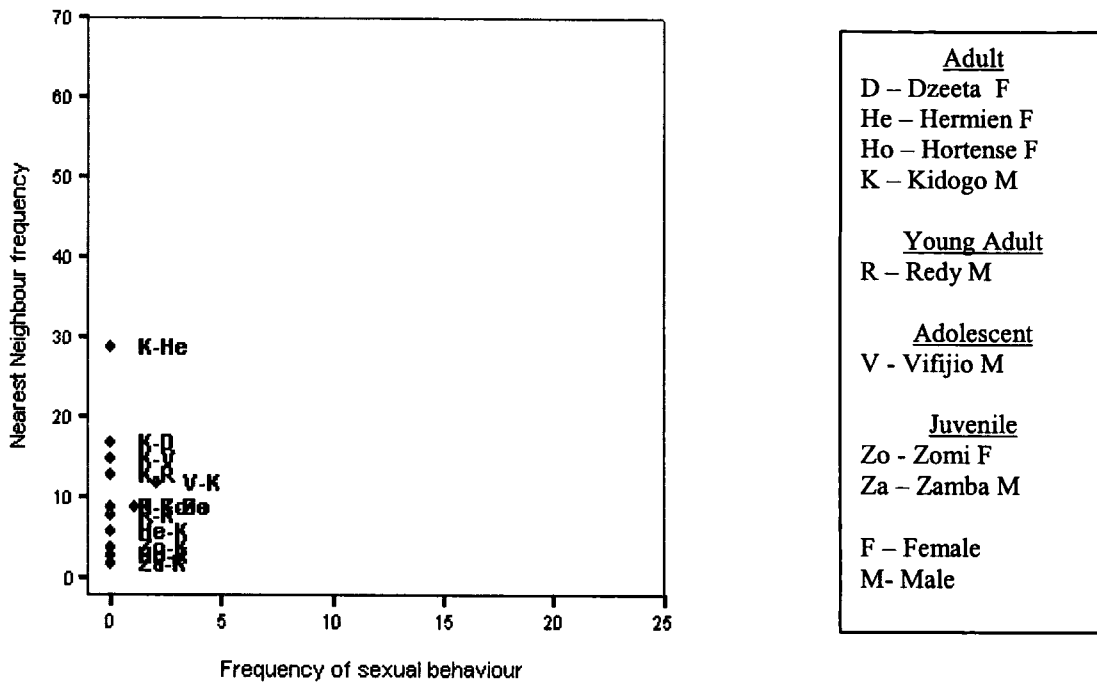


Figure 3.5h Frequency of each individual being Kidogo's nearest neighbour and socio-sexual partner

Kidogo was the oldest male, but the lowest ranking individual (evident from his interaction with group members) there was very little contact, either as NN or socio-sexual partner with any individual. Kidogo was always on the periphery of the group and the only relatively frequent NN was Hermien, although given Kidogo's peripheral position the closest NN may have been several metres away. The only socio-sexual behaviour occurred with Vifijio and once with Hortense, therefore the results do not support the prediction.

Vifijio is the young adolescent male in the group and the son of Hortense. Socio-sexual behaviour was overall low except for contact initiated by Vifijio with Dzeeta. Dzeeta did not initiate or play an active role in socio-sexual behaviour. These individuals were not particularly frequent NN, the most frequent to Vifijio being his brother Redy and mother Hortense. Socio-sexual behaviour occurred briefly with several group members, but all were infrequent NN's and for Vifijio the results do not support the prediction.

Vifijio : Comparison of Nearest Neighbour and Sexual Behaviour

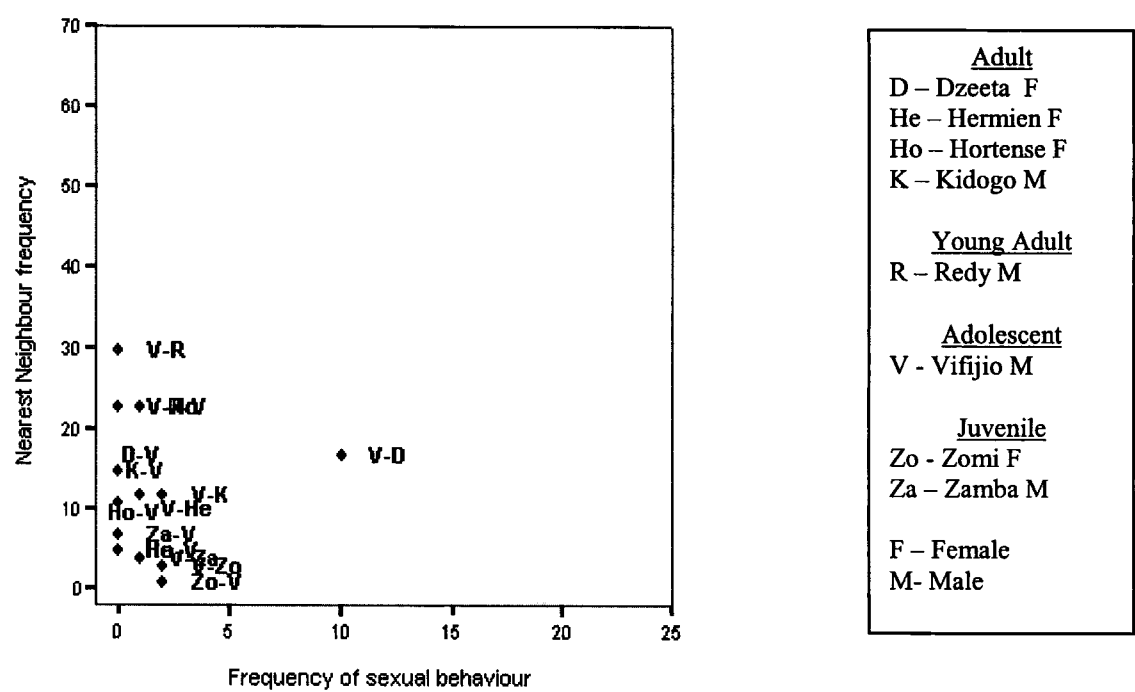


Figure 3.5i Frequency of each individual being Vifijio's nearest neighbour and socio-sexual partner

Zomi : Comparison of Nearest Neighbour and Sexual Behaviour

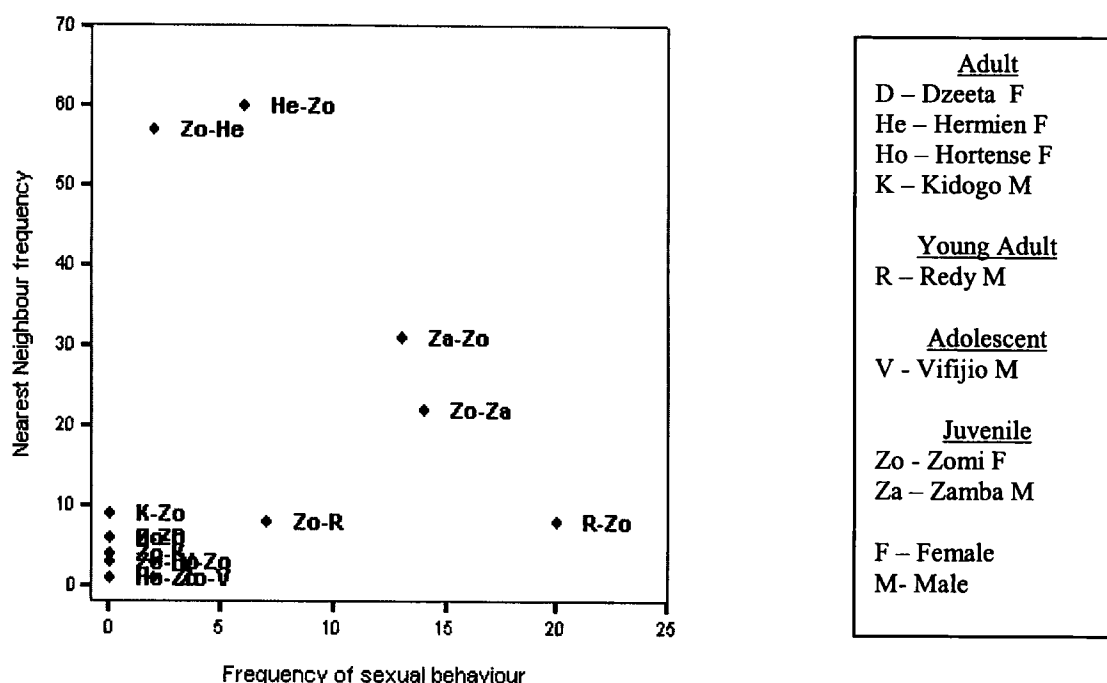


Figure 3.5j Frequency of each individual being Zomi's nearest neighbour and socio-sexual partner

Zomi, the juvenile daughter of Hermien was, along with Zamba, the individual most frequently involved in socio-sexual behaviour. The scatterplot above clearly shows this with Redy being Zomi's most frequent socio-sexual partner, but a very infrequent NN. With Zamba, Zomi initiates and receives socio-sexual contact and he is also a frequent NN, the most frequent apart from Zomi's mother Hermien who is by far the most frequent NN. Taking only Hermien, Redy and Zamba into account there is a relationship between NN frequency and socio-sexual behaviour frequency, the most frequent NN has the least socio-sexual contact and this increases the less frequent a NN is. Other individuals in the group are all very infrequent NN and socio-sexual partners. The results are unclear for Zomi but tend not to support the prediction, with the exception perhaps, of Zamba.

Zamba follows a very similar pattern to Zomi, apart from the interaction with Redy where there is little socio-sexual contact and Redy is a very infrequent NN to Zamba. Zamba's mother, Hortense is his most frequent NN and although socio-sexual contact occurs between them it is infrequent. Zamba's most frequent socio-sexual partner is Zomi, who is also a frequent NN. This can probably be attributed to age, both play together a lot of the time and socio-sexual behaviour is an integral part of this play. As with Zomi, interaction with other group members is very limited and all are infrequent NN and socio-sexual partners.

Zamba : Comparison of Nearest Neighbour and Sexual Behaviour

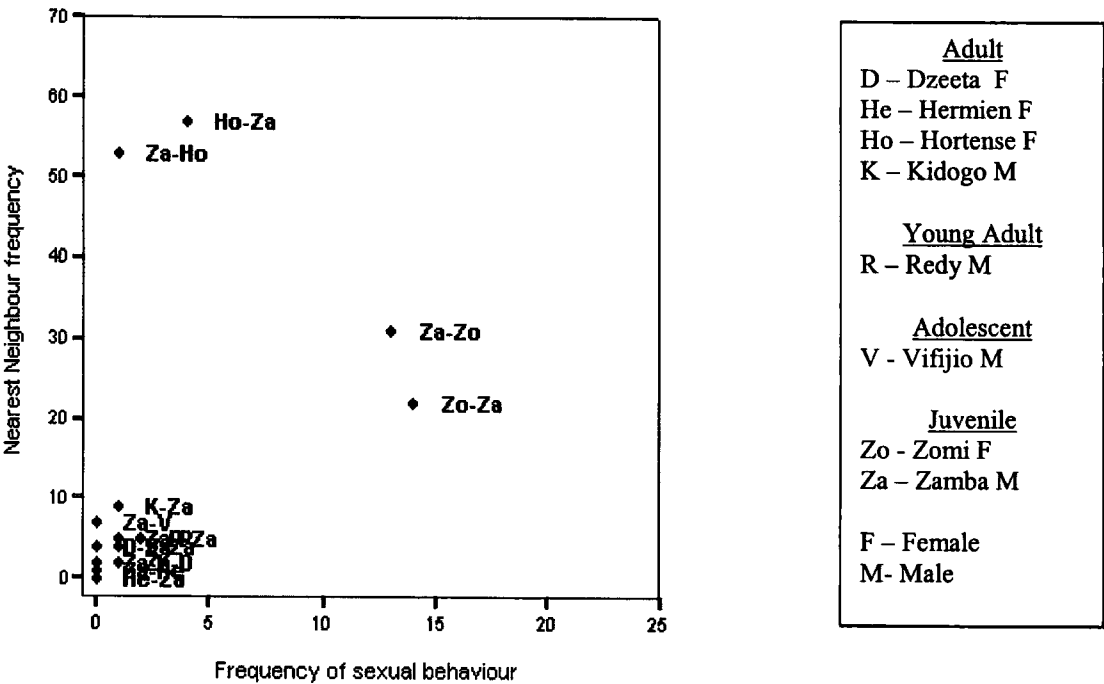


Figure 3.5k Frequency of each individual being Zamba's nearest neighbour and socio-sexual partner

Zamba's results closely match those of Zomi and do not support the prediction except, possibly Zomi, but as both these individuals are juveniles the results are difficult to analyse.

Hypothesis 4 Prediction 2: Individuals who are frequent socio-sexual partners will also be frequent grooming partners.

As with the previous prediction, a bivariate correlation was completed and there was found to be no correlation. Scatter plots illustrate the relationship between the frequency of each individual being the socio-sexual partner and grooming partner of another. The positions of initials in the following scatterplots are not related to initiator and receiver and solely represent the frequency of occurrences between two individuals.

Dzeeta : Comparison of Grooming and Sexual Behaviour

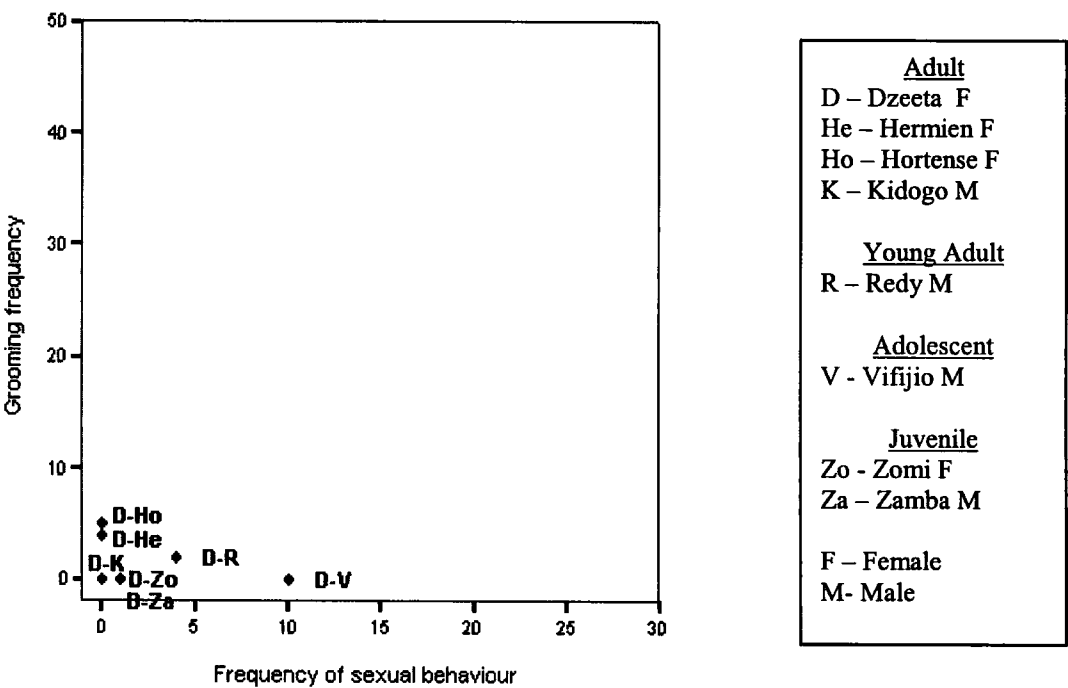


Figure 3.5k Frequency of each individual being Dzeeta's grooming and socio-sexual partner

Overall grooming and socio-sexual contact were very infrequent and for Dzeeta grooming interaction with the two adult females, Hermien and Hortense was also very infrequent. Also with both of these individuals there was no socio-sexual contact at all and for

Dzeeta a relatively frequent grooming partner is not a relatively frequent socio-sexual partner. The most frequent socio-sexual contact was with Vifijio, although Vifijio always initiated this and there was no grooming interaction between them. The results therefore for Dzeeta do not support the prediction.

Hermien : Comparison of Grooming and Sexual Behaviour

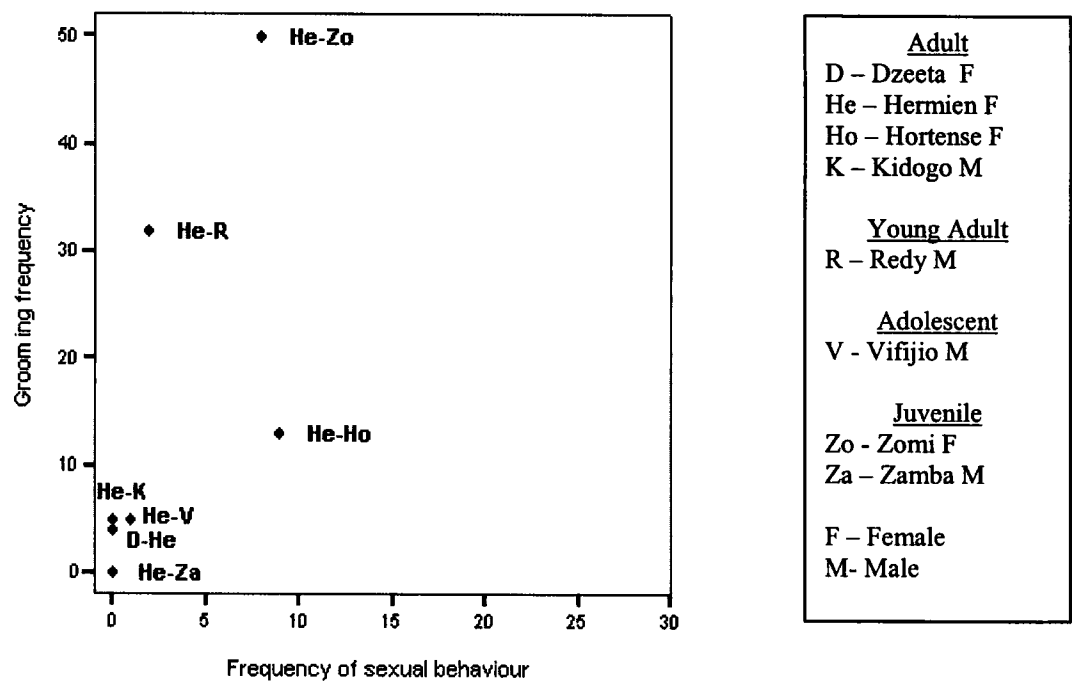


Figure 3.5m Frequency of each individual being Hermien’s grooming and socio-sexual partner

For Hermien grooming interaction was focused mainly on two individuals, Zomi her daughter and Redy the dominant male. Grooming interaction with Zomi was by far the most frequent and this was to be expected given the close mother-offspring bond. Socio-sexual behaviour between them was also relatively frequent given the low occurrence overall. Redy was a very infrequent socio-sexual partner, but very frequent grooming partner. The frequent grooming between Redy and Hermien is probably because she is the only unrelated receptive female in the group and therefore a possible mating opportunity. Hortense was a relatively

infrequent grooming partner, but the most frequent socio-sexual partner and out of all the adults Hermien and Hortense were the most frequent socio-sexual partners.

Hortense : Comparison of Grooming and Sexual Behaviour

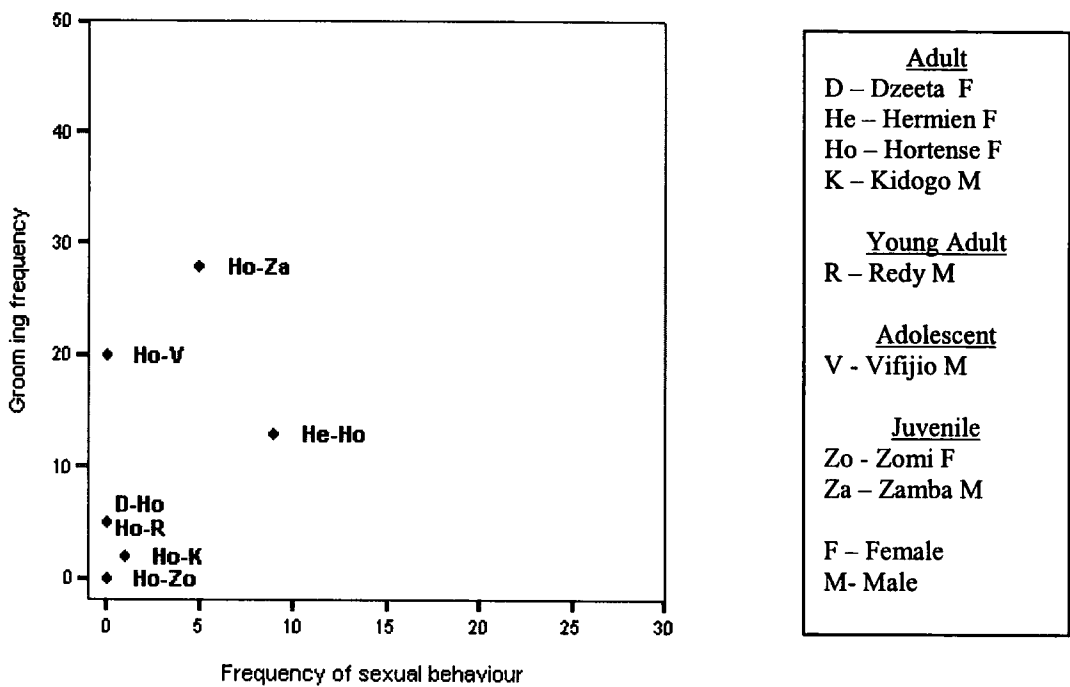


Figure 3.5n Frequency of each individual being Hortense’s grooming and socio-sexual partner

For Hortense the overall grooming frequency is much less than that of Hermien, especially with Zamba her juvenile son, although socio-sexual behaviour between them is similar to that found between Hermien and Zomi. Nevertheless grooming was most frequent between Hortense and Zamba, closely followed by Vifijio, Hortense’s adolescent son. There was no socio-sexual contact between Vifijio and Hortense, which would be expected. With Hortense’s other son Redy there was also no socio-sexual contact but also interestingly very little grooming between them. Overall for Hortense frequent grooming partners are infrequent socio-sexual partners, with only Hermien having similar frequencies. The results do not support the prediction.

Redy : Comparison of Grooming and Sexual Behaviour

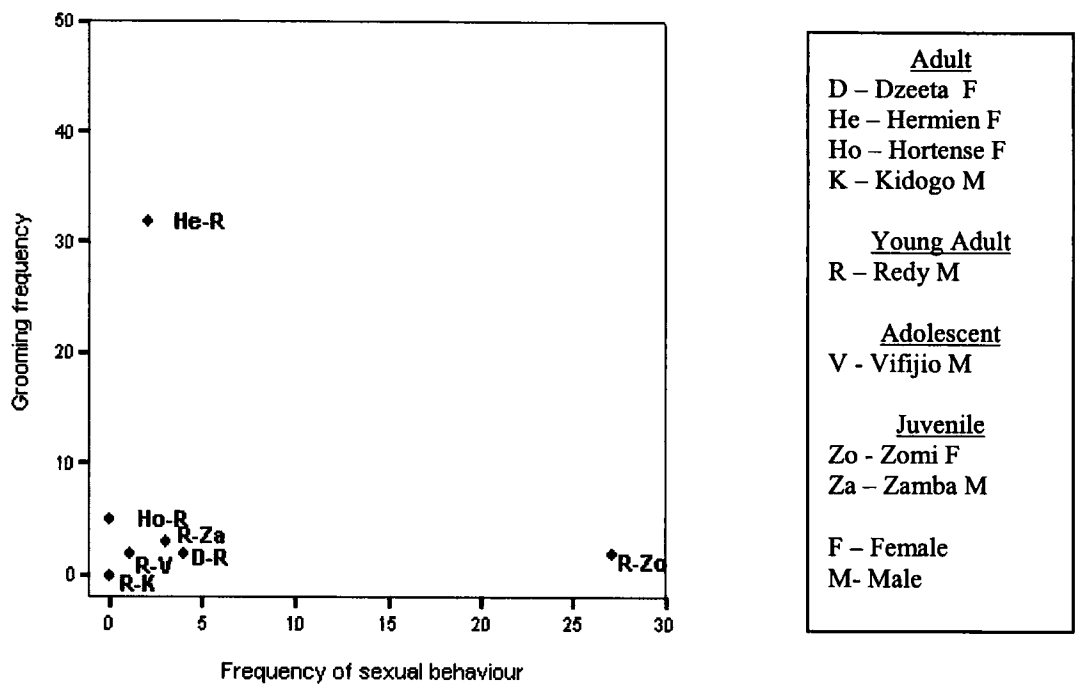


Figure 3.5o Frequency of each individual being Redy's grooming and socio-sexual partner

Redy has a clearly defined scatterplot with only two individuals that he frequently interacts with in grooming or sexual behaviour. Hermien is clearly the most frequent grooming partner, with all other individuals being very infrequent grooming partners. Socio-sexual contact with Hermien was very infrequent and this occurred most frequently with Zomi who was by far the most frequent socio-sexual partner. For Redy there is clearly no relationship between an individual being a frequent grooming partner and a frequent socio-sexual partner, and results show that the prediction is not supported.

For Kidogo, as with hypothesis 4, prediction 1, there is very little socio-sexual behaviour and grooming interaction is also very low. The only relatively significant grooming partner and to a lesser extent socio-sexual partner is Vifjio. Vifjio has double the grooming interaction with Kidogo than of any other individual. Again there is no relationship between an individual being a frequent grooming partner and a frequent socio-sexual partner and the results do not support the prediction.

Kidogo : Comparison of Grooming and Sexual Behaviour

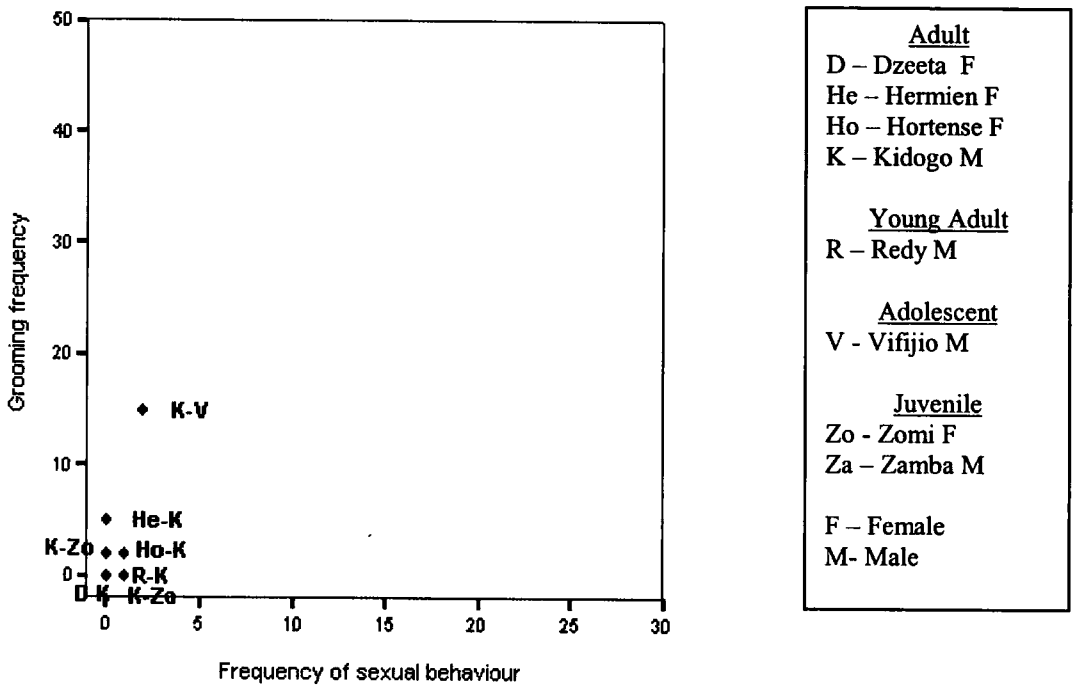


Figure 3.5p Frequency of each individual being Kidogo's grooming and socio-sexual partner

Vifijio : Comparison of Grooming and Sexual Behaviour

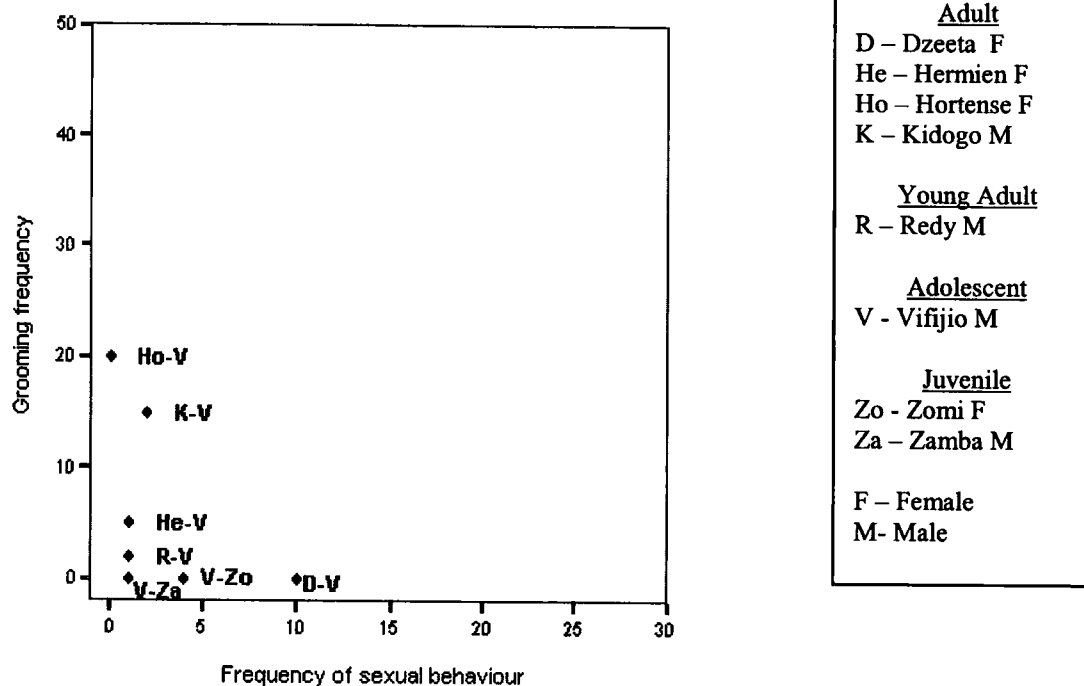


Figure 3.5q Frequency of each individual being Vifijio's grooming and socio-sexual partner

Vifijio also has a relatively low frequency of grooming interactions, with only two individuals having any relative frequency. Hortense, Vifijio's mother is the most frequent grooming partner, closely followed by Kidogo. Socio-sexual contact is non-existent with Hortense and infrequent with Kidogo, only with Dzeeta does Vifijio have relatively frequent socio-sexual contact, but no grooming interaction at all. Therefore for Vifijio frequent grooming partners are not frequent socio-sexual partners and the prediction is not supported by the results.

Zomi : Comparison of Grooming and Sexual Behaviour

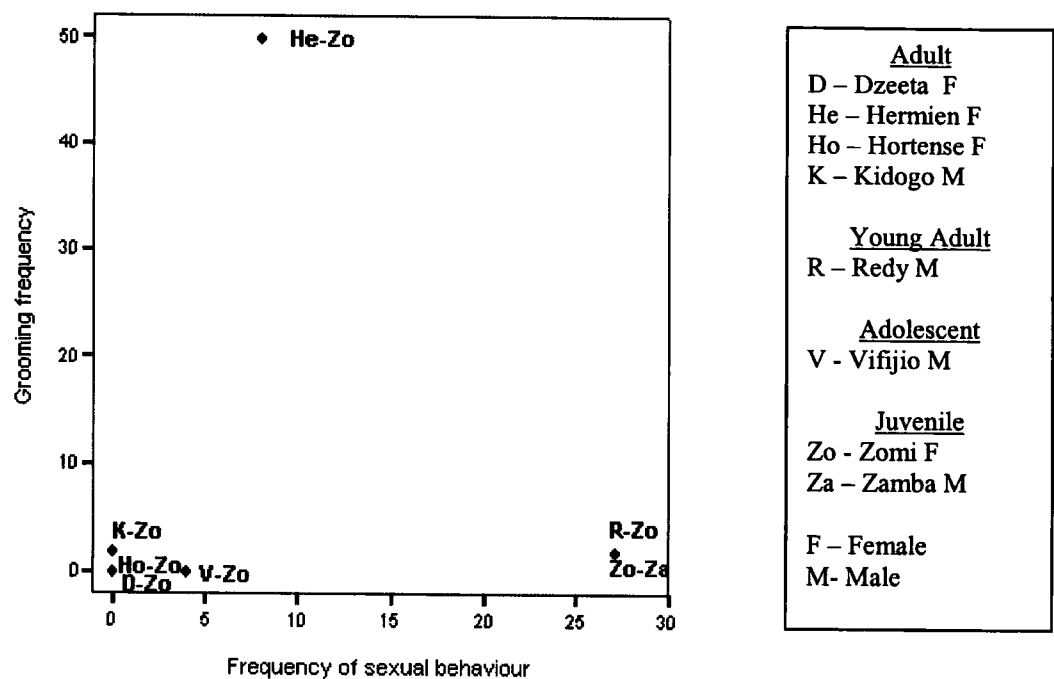


Figure 3.5r Frequency of each individual being Zomi’s grooming and socio-sexual partner

Zomi’s scatterplot closely resembles that of her mother Hermien. Hermien is Zomi’s only frequent grooming partner and a much less frequent socio-sexual partner. Redy and Zamba are very frequent socio-sexual partners with the same frequency but very infrequent grooming partners. Therefore for Zomi, frequent grooming partners are not frequent socio-sexual partners and vice versa and the results therefore do not support the prediction.

Zamba : Comparison of Grooming and Sexual Behaviour

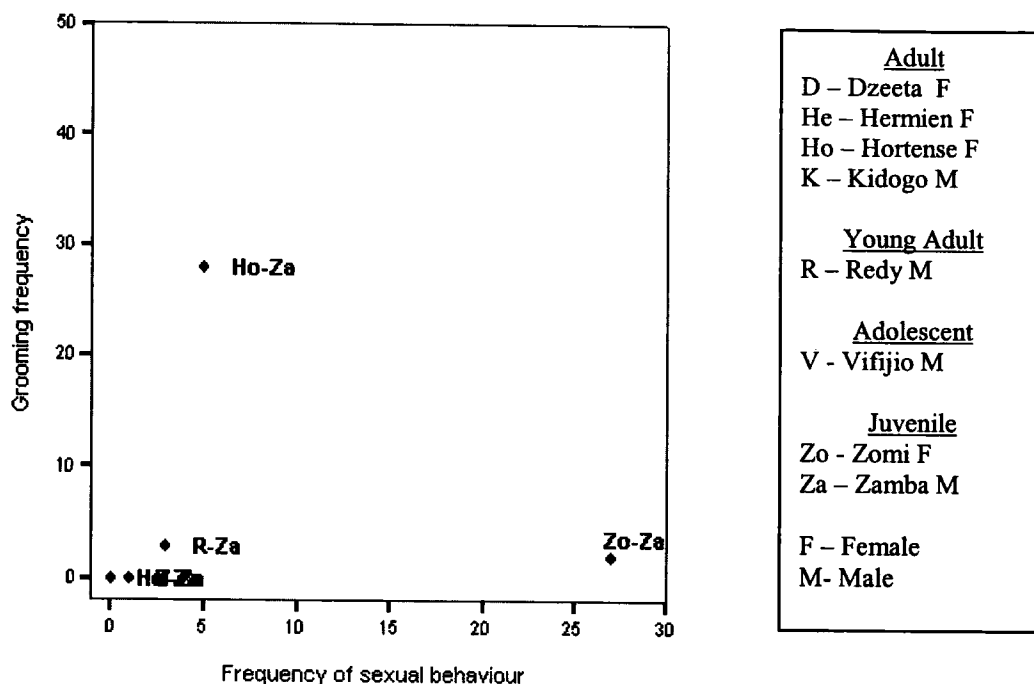


Figure 3.5s Frequency of each individual being Zamba's grooming and socio-sexual partner

Zamba's scatterplot is also similar to that of Zomi. Zamba's mother Hortense was the only frequent grooming partner and Zomi the only frequent socio-sexual partner. For all other individuals Zamba has very infrequent grooming or socio-sexual interactions. Therefore for Zamba, frequent grooming partners are not frequent socio-sexual partners and vice versa and the results do not support the prediction.

Prediction 4: That same sex socio-sexual behaviour would be more frequent between females, who form the core of bonobo society and less frequent between males

The results show a similar pattern to that found in the Twycross group. If the male is the initiator then almost exclusively the receiver is female. For females there is a higher preference for males than by chance, and female/female sex is less frequent than for the Twycross group, although females are far more likely than males to be receivers. For

Female/female socio-sexual contact 53% of all occurrences occurred between Hermien and Hortense, two adult females and the remaining 47% between Hermien and her juvenile daughter Zomi. For male/male socio-sexual contact all possible combinations were observed except between Redy and Kidogo. Therefore same sex socio-sexual behaviour between females is much higher than between males and this is significant, (Chi Sq = 27.825, df = 1, P = <0.001). Therefore the results support the prediction.

Sex of Initiator / Sex of Receiver				
		Sex of Receiver		Total
		Female	Male	
Sex of Initiator	Female	Count	17	27
		% within Female initiator	38.6%	61.4%
	Male	Count	55	8
		% within Male initiator	87.3%	12.7%
Total		Count	72	35
		% within Sex initiator	67.3%	32.7%

Table 3.5vii Sex of initiator and receiver of socio-sexual behaviour

Hypothesis 1: Reconciliation is in the form of socio-sexual behaviours	Prediction 1: Socio-sexual behaviour follows agonistic interactions	Prediction 2: Rates of socio-sexual behaviours increase after agonism	Prediction 3: Individuals frequently in close proximity sexually reconcile more than individuals who are not frequently in close proximity	Summary The results were not as predicted. Socio-sexual behaviour was not strongly related to agonistic interactions. There was no increase in socio-sexual behaviour following agonism and between individuals involved in agonism.
Hypothesis 2: Socio-sexual behaviours are a form of tension reduction	Prediction 1: In feeding situations socio-sexual behaviours occur more often between owners of food and bystanders than between bystanders	Prediction 2: The average duration of socio-sexual contacts would be expected to be higher during feeding, where tension is high, than in a non-feeding context	Prediction 3: Socio-sexual behaviour will be frequent between different age categories to reduce tension	Prediction 4: Initiation of socio-sexual behaviour will be frequent between same sex individuals (non-fertile pairs) Prediction 5: Assuming dominance plays a role in tension regulation, dorso-ventral and ventro-ventral mounting would be expected to be more frequent than non-mounting socio-sexual behaviour Hypothesis 2 Summary The results tend to support the predictions analysed. Socio-sexual behaviour was frequent and for a longer duration during tense social situations.
Hypothesis 3: Socio-sexual behaviours are an expression of social status	Prediction 1: Initiation of socio-sexual behaviour shows status-dependent asymmetries	Prediction 2: Individual spatial position shows status-dependent asymmetries, whether the individual is in the top or bottom position – horizontal only	Prediction 3: High status/low status dyads have socio-sexual contact more frequently and for a longer duration than high status/high status or low status/low status dyads	Hypothesis 3 Summary The results analysed support the predictions. High ranked individuals strongly preferred low ranked partners and took the dominant (top) position in socio-sexual behaviours. Interestingly mixed rank dyads had the longest duration of SSB, same sex dyads the least, supporting the expression of dominance.
Hypothesis 4: The function of socio-sexual behaviour is social bonding	Prediction 1: High frequency of socio-sexual behaviour between close spatial associates	Prediction 2: Individuals who are frequent socio-sexual partners will also be frequent grooming partners	Prediction 3: High frequency of socio-sexual contact between individuals of differing rank Prediction 4: That same sex socio-sexual behaviour would be more frequent between females, who form the core of bonobo society and less frequent between males	Hypothesis 4 Summary The results were mixed, supporting two predictions and therefore partly the hypothesis. The evidence is not as strong as for tension reduction or social status (Hypotheses 2 and 3).

Several factors that relate directly to the socio-sexual behaviour observed during the study are important for its validity. I will discuss this part subsequently.

4.1 The validity of functional analysis in captivity

Both of the study groups were relatively small in number and had a large proportion of related individuals. This highlights the particular difficulty of validating a functional analysis in captivity, where kin relationships, and their effect on many factors of behaviour, are likely to affect results. Kin relationships may affect for example, agonistic interactions, and an example from the Twycross group involved the dominant female Diatou supporting her son Ke Ke in agonistic interactions against the dominant male Kakowet II. Prior to Ke Ke's attempts to challenge Kakowet II for dominance, no noticeable agonism was observed between Diatou and Kakowet II. This clearly illustrates the effect kin relationships have on an individual's behaviour.

Both captive groups were relatively small in number and therefore had a limited range of age/sex combinations. As many of these individuals were related, this possibly reduces mating partners if there is a negative kin effect.

In comparing both the Twycross and Planckendael study groups, despite the difference in study time between them, it was clear that both groups had a similar range, frequency and distribution of socio-sexual behaviours. For both study groups the most frequently observed socio-sexual behaviours were dorso-ventral mounting closely followed by ventro-ventral mounting. An important issue is distribution similar to the wild or could part of the behaviour be artificial? Kitamura (1989) and Kano (1992), observations on wild bonobo groups, show that ventro-ventral mounting accounted for 29.1% of all mountings observed (1992:141).

Although this contradicts some captive studies, which differ markedly, where ventro-ventral mounting was 53% (Savage-Rumbaugh 1978) and almost 100% at San Diego Zoo (De Waal 1987). The San Diego Zoo individuals were adults, but infants at the time of capture and Kano suggests that 'socially deprived bonobos may not develop normal sexual behaviour' and therefore this does not mean that wild bonobos use this position (1992:142). On balance variations in socio-sexual behaviour do occur, but the overall frequency of ventro-ventral and dorso-ventral socio-sexual behaviours are similar.

For the Twycross group agonism towards zoo visitors on the one window side to their enclosure was very frequent. Usually this was as a result of agonism within the group being redirected towards people outside, or vice versa, or the group of gorillas in the adjacent enclosure. On other occasions no apparent trigger could be seen other than a large number of visitors at any one time. Nevertheless visitors may also cause agonistic interactions within the group. Socio-sexual behaviour following agonistic interactions was generally very low and lower still between the two former opponents, usually one former opponent and another individual uninvolved in the conflict. The only exception to this was at the end of the data collection where conflicts began to escalate due to a sudden attempted takeover of male dominance by the adolescent male Ke Ke. The results showed that the frequency of socio-sexual behaviour were not significantly different before or following an agonistic interaction.

4.2 Main findings and the meaning of the data in relation to function

Hypothesis 1: Reconciliation is in the form of socio-sexual behaviour

Reconciliation following agonistic interactions would be expected to be relatively high if socio-sexual behaviour was a form of reconciliation and three predictions were made for this hypothesis. The results were not as predicted, with only 5.9% of all socio-sexual

behaviours in the Twycross group occurring following agonism, although reconciliation may still be a function of socio-sexual behaviour. Although data for socio-sexual behaviours following agonism were limited, when comparing pre-conflict and post-conflict rates, it was found that post-conflict rates were higher and especially in the first 4 minutes following agonism. This does suggest a reconciliatory function. When the results for the post-conflict socio-sexual behaviour that occurred in these first 4 minutes was further broken down for the individuals (Fig. 3.iii, page 58) this showed several patterns. The most subordinate individual, the male Jasongo, neither initiated nor received socio-sexual contact following agonism. This is surprising as it would be expected that if socio-sexual behaviour was a form of reconciliation, that a low ranking individual like Jasongo would have a relatively high level of socio-sexual behaviour. Banya was also low ranking, yet had the highest frequency of initiation of socio-sexual behaviour following agonism. Therefore it appears that other factors are involved in the function of socio-sexual behaviour.

The relationship between nearest neighbour (proximity) and socio-sexual behaviour following agonism also did not support the hypothesis. It was expected that individuals frequently in close proximity would reconcile socio-sexually more than those infrequently in close proximity because frequent nearest neighbours would have more to lose following agonistic interactions. The results showed that nearest neighbours were more likely to be kin and these individuals infrequently reconciled socio-sexually. The only exceptions were found with Ke Ke and Banya, unrelated individuals, but both frequent nearest neighbours and socio-sexual partners following agonism (Figs. 3.1c & 3.1f, pages 62/65). This example tends to suggest that it is unrelated individuals, frequently in close proximity, that reconcile socio-sexually (Cords et al. 1996). Related individuals have less 'need' to socio-sexually reconcile, although it is also probable that kin have less agonistic interactions, therefore less

reconciliation. This example clearly illustrates the problems with small groups where many individuals are close kin.

For the Planckendael group data was insufficient for analysis of this hypothesis. Agonistic interactions were very low in this group and the limited time for data collection further compounded the problem.

Hypothesis 2: Socio-sexual behaviours are a form of tension reduction

Tension reduction was initially to be tested firstly in feeding situations in relation to agonism but because agonistic interactions were very limited during feeding, socio-sexual behaviour and the relationship with food ownership was analysed instead. Feeding situations provided the most data on socio-sexual behaviour between individuals in each group. Five predictions were made for this hypothesis.

For the Twycross group, analysis on food ownership proved an increased frequency of socio-sexual behaviour of individuals in possession of food, as opposed to individuals without food, but in a feeding context (page 75). This result supports the hypothesis that socio-sexual behaviour has a tension reduction function. Again data analysis was not possible for the Planckendael group as limited feeding sessions were observed and socio-sexual behaviour was infrequent during these.

Feeding situations, because of the increased tension, were also thought to increase the duration of socio-sexual behaviours during such times. The durations of each socio-sexual behaviour was recorded in seconds, throughout the study, and this enabled a comparison between particular occasions like feeding and at other times during a day.

The results for the Twycross group supported the hypothesis and durations of socio-sexual behaviours were higher during feeding than in a non-feeding context. The frequency of socio-sexual contact varied considerably between feeding bouts and this could be due to

various factors. Feeding occurred at differing times during the day and sometimes in the inside enclosure and sometimes outside. Also the foods given varied, from fruit juice to coconuts and probably had an effect on socio-sexual activity.

Data for the Planckendael group was again insufficient for analysis because socio-sexual behaviour during feeding was infrequent.

Individuals in both groups were from wide ranging age groups and as such it was predicted that socio-sexual initiation between these age groups would be higher than between same age group categories. Differing age groups also meant probably differing status within these individuals. For the Twycross group the results supported the hypothesis, more socio-sexual behaviour occurred between age groups than within age groups (pages 78-80). Several other factors could have affected the result. For example, kin relationships could have resulted in the high frequency because kin were present in each of the four categories (adult, young adult, adolescent and juvenile) and therefore it is difficult to speculate. Also the limited number of individuals probably affected results, especially the juvenile and adolescent categories with only one individual in each.

For the Planckendael group similar factors could have affected the results, with a similar number of individuals and a high number of kin. Although insufficient for analysis, the data shows a similar pattern to that of the Twycross group, with socio-sexual behaviour occurring between the age groups more frequently than within the age groups.

Socio-sexual behaviour between same sex dyads was predicted to support the function for tension reduction because competition between individuals of the same sex would be higher. This is especially between females, in competition for available resources and the need to reduce tension between possible allies. The same was thought to occur for males but less so because males are more peripheral and less bonded. In the Twycross group the results supported the hypothesis, with female/female socio-sexual behaviour frequent, but for males

same sex socio-sexual behaviour was too infrequent for analysis. Also the range of socio-sexual behaviour types was higher in females than for males. The Planckendael group data also supported the hypothesis; again female/female dyads were the most frequent. Overall the frequency and range for both sexes in Planckendael was higher than for the Twycross group, considering the difference in observation time. This especially applies to male/male socio-sexual behaviour. Although the results of both groups supported the hypothesis that the function of same sex socio-sexual behaviour is tension reduction, another possibility is that female/female dyads have more socio-sexual behaviour because females generally spend more time together, with their offspring. Males on the other hand spend less time in close proximity. This applied to both my study groups, with adult males in particular socialising very little between themselves.

The final prediction relating to tension reduction as a function of socio-sexual behaviour, presumed dominance was involved and therefore mounting socio-sexual behaviours would be more frequent than non-mounting. The assumption was that the dominant individual would mount the subordinate. For the Twycross group the data for mounting socio-sexual behaviours supported the hypothesis but insufficient data for non-mounting proved the results inconclusive. Mounting behaviours (ventro-ventral and dorso-ventral) were the most frequent socio-sexual behaviours in both groups and other non-mounting ones much less so. The results may be due to dominance or that mounting behaviours are 'preferred' and as such more frequent. A similar result was found for the Planckendael group and the hypothesis was again supported by the data.

Therefore the evidence from the results of both groups tends to support the hypothesis that socio-sexual behaviours are a form of tension reduction.

Hypothesis 3: Socio-sexual behaviours are an expression of Social Status

Rank analysis for the Twycross group was ascertained by agonistic interactions and displacement data, and this provided two categories, high rank and low rank, with three individuals in each. Three predictions were made for this hypothesis, which were supported by the data. There were found to be status-dependent asymmetries in initiation of socio-sexual behaviour, high ranked individuals had a strong preference for low ranked partners. This suggests that socio-sexual contacts function to show differences and re-establish rank status. The position of the initiator, whether in the top or bottom position of a socio-sexual dyad also showed that high-ranking individuals were always in the top position when initiating (page 89), low ranking individuals were not observed to initiate in the top position. This suggests socio-sexual behaviour functions as an expression of dominance, again supporting the hypothesis. The duration of socio-sexual behaviour in relation to rank dyads also provided some interesting analysis. Same rank dyads had the shortest durations of socio-sexual behaviour, whereas mixed rank dyads had the longest durations (page 90). The longest duration (average of 8.02 seconds) was a high ranked individual, Diatou, initiating socio-sexual behaviour with a low ranked partner, Banya. This also supports the hypothesis and suggests an expression of dominance.

Rank analysis for the Planckendael group was not possible as there were insufficient agonistic interactions and few displacements occurred. Also due to a recent change in group dynamics, previous references to group rank (Vervaeke 2000) were no longer applicable.

Hypothesis 4: The function of socio-sexual behaviour is social bonding

There were four predictions made for this hypothesis and for the Twycross group, two that were supported by the data. Two could not be tested statistically but graphs showing the relationships between two variables, socio-sexual frequency and nearest neighbour frequency and also socio-sexual frequency and grooming partner frequency were produced (Figs. 3.4a-o). Frequent socio-sexual partners were found to be infrequent nearest neighbours and also infrequent grooming partners. The data from both did not support the hypothesis. The data for individuals of differing rank having a high frequency of socio-sexual behaviour supported the hypothesis, especially initiations by high ranked individuals, but there was a preference for socio-sexual contact between different ranks. This suggests a possible bonding function within the group, but there could also be the possibility of dominance interactions. The prediction for female/female socio-sexual contact being higher in frequency than for males was also supported by the data. In the Twycross group male/male socio-sexual contact consisted of 3 occurrences, compared to 255 for females and this suggests that bonding between females is a function of socio-sexual behaviour.

The data for the Planckendael group are similar for the first two predictions and there was no relationship between socio-sexual behaviour and nearest neighbour frequency or grooming partner. The third prediction was not possible for the Planckendael group because rank status was unknown for the group. The final prediction was, as in the Twycross group, also supported by the data and similar results were found. Female/female socio-sexual behaviour was much higher in frequency than male/male dyads.

Social bonding as a function for socio-sexual behaviour was partially supported by the data from both groups but the evidence is not as strong as for tension reduction or as an expression of social status. These two hypotheses are well supported by the data and the most probable function(s) of socio-sexual behaviour in bonobos.

4.3 Comparison of the two captive groups

Both of my study groups had a similar age and sex composition, apart from the number of mature adult females, Twycross had just one (and two young adult females) and Planckendael had three. Planckendael also had two juveniles (whereas Twycross had one); a male Zamba and a female Zomi, only months apart in age and this provided some interesting data. One problem with any behavioural observation is time and early morning observations were not possible. In the wild 69% of copulations occurred from 5.30am to 9.00am and almost the same at the feeding site during the same time period and therefore this can be particularly difficult for researchers like myself (Kano 1992:149).

Observing male/female sexual mountings I found that they occurred in a wide range of social contexts but always the male was fully erect and thrusting was evident. This contradicts Furuichi (1992) where he suggests that non-sexual mounting during feeding or agonistic interactions is not “true sexual behaviour” in that no penile erection or intromission need have occurred (1992:180). For bonobos, with respect to form, sexual behaviour cannot be seen as distinct from social interaction and therefore I argue that to do so is meaningless. I did find that penile insertion was difficult to observe on many occasions, although it was probable that insertion took place almost always during mountings between males and sexually mature females. This should be noted that it might be even more difficult to accurately observe in the wild. I also noted each sexual occurrence, which involved individuals initiating and ceasing genital contact (Furuichi 1992:180). What Furuichi appears to miss is that such ‘copulations’ between males and females can also be a means of reducing tension or accessing food. For example in the Twycross group, sexual activity increased around feeding and all

combinations engaged in socio-sexual behaviour, some of which would be classified according to Furuichi as copulations and some non-sexual mountings (Furuichi 1992:180).

4.4 Comparison of the main findings in relation to other studies

The types of socio-sexual behaviour observed in both groups closely follow that of other studies of both captive and wild groups with the main difference being the relative lack of male/male socio-sexual behaviour. Adult males were limited to two individuals in each group, a young adult male and a more mature adult male and this may have had a bearing on results. In the Planckendael group the two males Redy and Kidogo were never seen in close proximity, all interactions were agonistic and as such any socio-sexual contact would not have been possible. In the Twycross group Kakowet II and Jasongo were also never observed in socio-sexual contact, although affiliative interactions occurred between these individuals, including grooming and play behaviour. No evidence was seen at all for rump-rubbing as described by Kano (1992) in either group and male/male socio-sexual behaviour only accounted for 1.8% of all socio-sexual behaviour in the Twycross group and a slightly higher 12.7% for the Planckendael group, although this mainly consisted of immature individuals. The results tend to be supported by findings from de Waal's (1995) study on captive bonobos at San Diego Zoo, and de Waal also found oral sex occurred almost exclusively between juveniles (although the group de Waal observed oral sex in was an only juvenile group). Adult/juvenile oral sex was observed between a mother and juvenile daughter, Hermien putting her daughter Zomi's clitoris in her mouth on several occasions while playing. I have not found any reference to this form of oral sex in any of the literature and oral sex is always described as being performed on males (de Waal 1995:43). Mouth kiss was also found between this mother/daughter pair, again in a play context and also between the two juveniles Zomi and Zamba, as de Waal also found (1995:43).

The socio-sexual behaviour of juvenile and adolescent individuals in both groups provided interesting data. In each group only one male and one female were present, the adolescent male Ke Ke and juvenile female Yasa in Twycross and the two juveniles Zomi and Zamba in Planckendael. Therefore same sex juvenile/adolescent socio-sexual behaviour was not possible. Mother/juvenile socio-sexual behaviour did occur, although infrequently, in both groups and this included both mother/son and mother/daughter dyads. Socio-sexual behaviour between a father and juvenile daughter was observed in the Twycross group on 3 occasions and all in a play context. This was not possible in the Planckendael group, as the father of the two juveniles had died.

Interference of socio-sexual behaviour by non-participating individuals was very infrequent in both groups. Juveniles were by far the most frequent individuals to do this and usually involving their mother being mounted by a male. In the Twycross group Yasa in particular would climb onto her mother, Diatou's back when her father Kakowet dorso-ventrally mounted Diatou. Kichele, Diatou's eldest daughter would stand and present to Kakowet but placing her rump on his back, almost like the male rump-rump rub (not observed in either group). This is supported by evidence from Kano (1992) where interference by other bonobos was very low, around 7% of all mountings and juveniles showed the strongest interest in mountings, clinging to the belly or back of either partner (1992:145/6). "Multi-individual copulation" was described by Kano and found to occur in varying combinations, a male dorso-ventrally mounting two GG rubbing females for example. This was uncommon, and most frequent in adolescent males and this behaviour was not observed in either study group (1992:149). Kitamura (1989) mentions an occurrence where two males ventro-ventral mounted and both had pelvic thrusts, and where 'the genitals are presumably in contact' (1989:57). I have seen this occur once in the Twycross group, with Ke Ke and Jasongo

ventro-ventral mounting, both had pelvic thrusts and their penises were rubbed together and no insertion took place.

I observed what many researchers including de Waal (1995), Kano (1992) found, that when food was provided the bonobos became very excited and initiated socio-sexual contact with each other, followed by peaceful feeding. Unlike de Waal I witnessed very little food sharing, de Waal found subordinate individuals could take food from more dominant ones following socio-sexual behaviour (de Waal 1987:50), yet I found that individuals that possessed food often parted without any exchange.

Regarding socio-sexual initiation, both sexes were seen to initiate socio-sexual contact, this contradicts Kitamura (1989) who, although mentioning that a 'female's efforts' could lead to copulations, states that a male is usually seen as the initiator in sexual contact with a female because he has an erect penis (1989:51). My results disagree with this, a male approaching a female to initiate sex is one thing, but the fact this male has an erect penis is irrelevant. I have seen on several occasions a female approach a male and initiate socio-sexual behaviour with the male, who has an erect penis but was not displaying to the female (he was facing the other way) and was therefore the receiver. Male bonobos were observed with an erect penis during numerous social activities including play and during feeding situations. This evidence is supported by results from other researchers, mentioned earlier, including Kano (1992), Ihobe (1992), Furuichi et al. (1994).

4.5 Reconciliation.

Reconciliation is defined by de Waal and van Roosmalen (1979) as "any friendly, sexual, playful or other non-agonistic body contact between two former opponents within 10 minutes after their conflict, whether the conflict was food related or not" (1979:55). I disagree with such a definition in so much as reconciliation can occur in a much longer time frame

than 10 minutes and would therefore not be included within this definition. I have witnessed in the Twycross group after a group agonistic interaction involving almost all group members, the group came together approximately half an hour following this and began grooming. Up until then no reconciliation had occurred between former opponents.

Reconciliation is suggested to take the form of socio-sexual behaviour, which could be used by individuals to reconcile following agonism and de Waal found that many instances of genital massage occurred in this instance. With such agonism reducing functions this could explain the frequency and age/sex combinations and why such behaviour is not restricted to male/female pairs (de Waal 1987:50). My results found that reconciliation was infrequent following agonistic interactions and generally low overall, and the results found are supported by the data from Hohmann and Fruth (2000:112). Hohmann et al. (2000) found that some rates of socio-sexual behaviour increased following agonism, but not all, out of 26 post-conflict socio-sexual contacts only 15 involved former opponents (2000:112). A large amount of socio-sexual behaviour occurred independently of any agonistic encounters and agonistic interactions were generally low (Hohmann et al. 2000:113). Although this does not necessarily mean that socio-sexual behaviour does not have a reconciliatory function.

4.6 Agonistic interactions and socio-sexual behaviour

Regarding agonism between the two *Pan* species the aggressor and target appear to be opposite, with chimpanzee females being the target for agonism by the males, whereas evidence from the wild and captive bonobo groups has shown males rarely agonise females and are in fact attacked and sometimes seriously injured themselves. In Parish's (1996) article several descriptions of female attacks on males are documented and almost all initiated by adult females. In the Stuttgart bonobo group in Germany Masikini, possibly Diatou's father,

was attacked and bitten on the toes and penis, and in San Diego the male Akili was bitten on the toes, ears and testicles (Parish 1996).

Evidence from wild studies (Furuichi 1989, Kano 1992) supports this. Although female bonobos are dominant and will attack a male, there is usually a reason for this and there is not the brutality seen in chimpanzees (Goodall 1986) where males can seriously injure a female or another male, with a lot more aggression. The reasons for females cooperating to aggress males are not totally clear, though it may be due to external influences causing tension in the group. I observed an attack at Twycross apparently initiated by the appearance of a large group of school children in front of the bonobo enclosure, one child in particular they took a dislike to and charged at the glass, followed by an attack by the 3 adult females on Jasongo, redirected aggression. Alternatively it may be due to pestering by males, in the Planckendael group where Hermien and Hortense cooperated to aggress Redy who was pestering Hermien. The function may be to intimidate males as chimpanzee males do with females (Goodall 1986) to increase submission and compliance with the interests of the females. An example is the previously mentioned attack by Banya on Ke Ke who had been pestering Banya for some time and who ceased pestering for a considerable amount of time after the attack (Parish 1996:80).

Ke Ke is an adolescent but is already trying to take over the dominant male position from Kakowet II, his father (pers. comm.). He is very young to be attempting this (8 years old) and captivity may be a possible factor in this situation, although his mother's influence and high status are also probably factors. The same scenario is applicable to Redy in the Planckendael group, also a young male, with his mother in the group, and he is very clearly dominant. Ke Ke was assisted in agonistic interactions against Kakowet II by Diatou his mother, and also the dominant female and she is even more protective given his relatively young age. Had this occurred several years later when Diatou was less protective, the

situation may have been different, although evidence from the wild suggests this can occur in the wild as well. Furuichi et al (1994) found that between the two *Pan* species, the main difference in dominance status is the effect mothers have on their sons' status. In both species adult males have a higher rank than adolescents, but for bonobos relatively young individuals can occupy high rank if their mothers are present in the group (Furuichi 1994:221). Kano (1992) also supports this noting in several cases that a young male rapidly increased in rank due to his mother's influence (she was also high ranking). This contrasts with chimpanzees where age is usually the main factor and males older than 20 occupy higher ranks and this is not related to their mother's presence in the group (Goodall 1986, Hayaki et al. 1989).

This situation was reflected in the Planckendael group where the older male Kidogo was clearly the most subordinate and appeared visibly afraid of Redy, but with nowhere to go and no other males as potential allies the situation was unlikely to change. Immediate reconciliation in the Twycross group overall was also low, grooming was observed on several occasions between former opponents but often half an hour or more after an agonistic interaction. Socio-sexual behaviour during and following several agonistic incidents occurred, but always involving the target of aggression and a bystander and points more to a tension reduction function.

The rate of socio-sexual behaviour also appears to bear little relation to agonism, occurring in similar frequencies before and after agonistic interactions. This suggests that for the Twycross group socio-sexual behaviour is not related to reconciliation and conflicting individuals are no more likely to reconcile using sex. This is in contrast to de Waal (1987) where he found that, as he expected agonistic interactions increased at feeding time; it was higher than the time period immediately before feeding and throughout the day generally (1987:328). Although the manner of feeding was different, in de Waal's San Diego groups branches and other edible plants were provided in a bundle to 'stimulate competition and

sharing' as this type of food 'induces only a mild level of competition' (1987:322). This was not the case in Twycross where food was liberally scattered, but even when the food was piled together competition was minimal. Branches were not given during my observations, as this was felt by the keeper to create increased agonism within the group, and given the group dynamics and increasing tension this type of food provisioning was therefore not possible. Other foods such as coconuts and pineapples were given, but not where food could be largely monopolised.

In the Twycross group much of the agonism centred on Ke Ke and Banya, often escalating and involving the whole group. Ke Ke was an adolescent male and Banya a young adult female, the only unrelated female to Ke Ke in the group. Probably due to this and Banya's young age and low status Ke Ke frequently pestered Banya, who often appeared visibly distressed and vocalised frequently. Almost always Banya would eventually retaliate and attack Ke Ke who would back down. Diatou would not support Banya in agonism against Ke Ke as he was her son, but would often agonise the lowest ranking male Jasongo, who frequently became the target of agonism (redirected aggression) or less frequently the dominant male Kakowet II.

4.7 Tension reduction

Tension reduction was first described by de Waal (1989), the theory that bonobos 'use' sex to diffuse tension in stressful social situations such as feeding and group conflicts. The statistical tests completed for this hypothesis showed positive results and support the use of socio-sexual behaviour as a means to reduce tension. Food ownership was found to be minimal in the majority of feeding situations, although individuals in possession of food were far more likely to participate in socio-sexual activity than those without food. When socio-sexual behaviour occurred where at least one individual had food the result proved that 81.5%

of all interactions in a feeding context included at least one individual in possession of food (page 68). Feeding resulted in a considerable amount of socio-sexual activity between all members of the groups in an intensely excited state and the duration of socio-sexual activity during such situations was found to be longer overall than in a non-feeding context. This suggests an increased 'need' for socio-sexual behaviour in times of intense excitement. De Waal found that agonism increased following food provisioning, that grooming decreased and that other contacts such as socio-sexual behaviour increased after food provisioning and agonism (de Waal 1995:50). De Waal also deduced that food or feeding does not 'cause' socio-sexual behaviour as this also occurred following agonism and suggests that socio-sexual behaviour is a tension reduction mechanism (de Waal 1995:50). An example taken from video footage of a feeding occurrence in the Twycross group shows Ke Ke the adolescent male who had been pestering Banya for sex, initiating frequently and being ignored. Eventually Banya charged and kicked Ke Ke hard, pushing him backwards, he then immediately ran over to his younger sister Yasa and ventro-ventral mounted her, all the while looking across at Banya.

The results are supported by evidence from de Waal (1987) where he concludes that providing food increases agonistic, socio-sexual and affiliative behaviour (except grooming). He also found that many of the socio-sexual interactions occurred between owners of food and bystanders (individuals without food). Begging was more likely from low ranking individuals, whereas high-ranking individuals would use agonism. De Waal found that food transfer occurred in 63.5% of interactions (1987:328/9). This was not witnessed in significant amounts at Twycross, probably because of an abundance of food that was evenly distributed and individuals took whatever they wanted, the only individuals to attempt to steal food or beg were Yasa and Ke Ke, and mainly off their older sibling Kichele or their mother Diatou. This observation makes de Waal's findings, cited previously, less surprising as being different from my results. Although begging was very infrequent, on one occasion Ke Ke was seen to

beg from his mother who refused, he subsequently had a tantrum, screaming and throwing himself on the floor, but he received no food.

GG rubbing as supported by de Waal (1987), Kuroda (1980) and Parish and de Waal (1996), allows cooperative female/female interaction and reduces tension. Results from my study also support tension reduction as a function of socio-sexual behaviour. Parish suggests this is necessary to form bonds and coalitions who lack the benefit of shared genes as male chimpanzees do. The ultimate result is that female bonobos gain greater access to resources and this increases their reproductive success (Parish 1996:76). Parish compared the age of first reproduction between captive bonobos and chimpanzees and it was found that bonobo females reproduced 1.5 to 4 years earlier than chimpanzee females. This is more difficult to deduce in wild groups and is therefore not conclusive (1996:82).

For the Planckendael group, certain foods were monopolised, especially food items placed inside plastic bottles together with wood wool. These were suspended in a wire cage running almost the length of the top of the enclosure. The bottles had to be manipulated with fingers or sticks to receive any food. Here Hermien always monopolised the food, with Hortense often beside her together with their two juveniles. The males had limited access, although some always fell to the floor where the males would gather. I did not witness any sharing of food except between mothers and offspring.

Socio-sexual behaviour between the various age group categories proved significant in the Twycross group with a high frequency between the age groups. The young adults were the most frequent initiators and receivers in the group, although this did contain the most individuals of all the categories. It was apparent that individuals tended to initiate with those of a different age group rather than an individual from the same age group. The results, although significant are limited by the number of individuals within each age group and could possibly be very different in wild populations.

For the Twycross group, same sex socio-sexual behaviour was frequent between females, but very infrequent between males. This supports both captive and wild studies with regard to adult females, but adult male socio-sexual behaviour in the wild was relatively frequent (Kano 1992) and the problem appears to be agonism and competition that prevents these males from interacting. In the Planckendael group same sex socio-sexual behaviour was less frequent for both males and females than was expected, female socio-sexual interaction was limited with no same sex socio-sexual behaviour observed for Dzeeta. The two adult males Kidogo and Redy were never seen to interact, Kidogo was twice the age of Redy but smaller and appeared to be visibly afraid of him, each time Redy approached anywhere near Kidogo, Kidogo would move out of the way and keep as much distance between himself and Redy as possible.

Mounting socio-sexual behaviours were by far the most frequent socio-sexual behaviour seen in both groups, strongly suggesting a dominance issue both within and between the sexes. Dominant individuals especially would dorso-ventral mount subordinate individuals and this was particularly evident in the Twycross group where Diatou would dorso-ventral mount Banya, together with pelvic thrusting, not the side-to-side motion usually seen with GG rubbing, and she was the only female observed exhibiting this behaviour.

Another possible socio-sexual behaviour observed in both of my study groups was 'nipple rubbing'. This was a very infrequent behaviour, but my findings are supported by de Waal (1995) who suggested this behaviour has a self-reassurance function during tense events. De Waal found that almost all of the occurrences were due to one adolescent male, but I found adult males and females both exhibited this behaviour, usually during agonistic interactions (de Waal 1995:45).

The duration of socio-sexual behaviours was found to be longer in a feeding context where the group was tenser, than in a non-feeding context where individuals were much calmer. The results strongly suggest that socio-sexual behaviour is used to reduce tension.

4.8 Social Status

Ascertaining rank was extremely difficult due to the low levels of agonism observed within both study groups (although it can be frequent in specific circumstances). Agonistic interactions together with displacement activities were used to deduce rank for the Twycross group (Table 3.3i, page 86). A considerable period of time was necessary in order to collect sufficient data for this and therefore rank analysis was impossible for the Planckendael group.

In the Twycross group the juvenile female Yasa was found to have insufficient data for agonism and displacement and she was omitted from all rank related analysis. The Twycross group overall was shown to have a non-linear hierarchy with a definite dominant and low ranking individual, but individuals in-between these were not clear and fluctuated. Data concerning rank related initiations (page 88) show that there was no difference in the frequency of low and high-ranking individuals in initiating, by far the most frequent was initiation between individuals of differing ranks, especially high rank initiating with low ranked individuals. This contradicts Hashimoto (1994), who found that the subordinate individual initiates with the dominant individual. Banya would infrequently initiate socio-sexual contact with Diatou. The position taken by the initiator and receiver also varied with both assuming the top and bottom position.

The relationship between rank and sexual position, whether top or bottom found that there was a considerable difference between the two ranks and the most frequent position. I found that high ranked individuals most frequently initiated and in the top position with the

reverse for low ranked individuals. Therefore the results strongly suggest that the position an individual assumes during socio-sexual behaviour is closely related to dominance.

I did find that for the Twycross group individuals of differing ranks who engaged in socio-sexual mounting had more frequent occurrences and for a longer duration than individuals of the same rank. What might be expected is that individuals close in rank might have more conflict to sort out these differences with socio-sexual behaviour as well as in agonistic interactions. The longest duration and highest frequency of socio-sexual behaviour occurred when high ranking individuals initiated sexual contact with low ranking individuals. This suggests that possibly the greatest tension is between individuals of differing rank and that socio-sexual contact is therefore of a longer duration than two individuals of similar rank. Or possibly this is related to dominance with the dominant initiators reinforcing their status to the subordinate receivers.

4.9 Social bonding

Individuals who were frequently in proximity were found to be infrequent socio-sexual partners, which was probably due to such individuals being close kin. Although in the Twycross group the only individuals who were both relatively frequent nearest neighbours (NN) and socio-sexual partners were Ke Ke and Yasa, the two youngest individuals and brother and sister. In the Planckendael group the two juveniles Zomi and Zamba were also relatively frequent NN and socio-sexual partners but were not related. The socio-sexual behaviour between these individuals was mostly during play and it appears that close spatial associates are also frequent socio-sexual partners only for young individuals. Therefore, in captivity, with limited group size, half of who were related, overall the individuals in frequent proximity were not frequent socio-sexual partners.

The relationship between grooming partners and socio-sexual behaviour showed a similar pattern, that overall for individuals in both groups, frequent grooming partners were infrequent socio-sexual partners and vice versa. There were exceptions, in the Planckendael group the two mother juvenile dyads, Hermien and Zomi and Hortense and Zamba were not surprisingly very frequent grooming partners, although usually grooming directed from mother to juvenile. Both females were also relatively frequent socio-sexual partners and although the overall socio-sexual frequency was low, the socio-sexual contact was relatively high for both mothers and juveniles. In the Twycross group grooming and socio-sexual behaviour between Kichele and Yasa (half sisters) was relatively frequent, the only pair in the group to do so. As with Ke Ke, Kichele frequently associated with Yasa, but whereas for Ke Ke grooming frequency was low, for Kichele this was relatively high.

Franz (1999) tested Seyfath's (1977) model of rank related grooming attractiveness on 4 groups of captive bonobos, including the Planckendael group. According to this model 'higher ranking individuals should receive more allogrooming from lower ranking individuals, than vice versa' (Franz 1999:527). Data were collected in 1993 and the rank then was, in order of dominance: Dzeeta, Hermien, Desmond, Hortense, Kidogo – Redy was then an infant (Franz 1999:528). Franz represented the linearity of dominance hierarchies within each group via Kendall's Index of linearity (Appleby 1983). Franz found that the Planckendael group had a significant linear dominance structure, adult males are usually subordinate to adult females, but at Planckendael Desmond was of higher rank than Hermien. This was the only exception Franz found out of the 4 groups studied (1999:531). The highest grooming rates were between adult male/adult female dyads, followed by adult female/adult female dyads, with subadult males showing the least rates overall (1999:532).

Parish (1996) wanted to study whether female bonobos affiliate (maintain bonds) as opposed to what Wrangham (1986) suggests that females tolerate each other, using tension

reduction mechanisms (1996:66). Parish found that females associated far more with other females than males, around three quarters of the time. Females far more often terminated an association with a male than vice versa, also supported by de Waal (1995) cited in Parish (1999:67). I found a similar pattern in both group of bonobos, females were often in close proximity, even while resting or sleeping, whereas males frequently spent more time apart.

Parish studied 'fishing behaviour' at artificial termite sites (for honey or milk powder). Monopolization of the feeding site by females was a key factor. I had wanted to emulate this with the Twycross group, but unfortunately this was not possible at the time. Although when preferred foods like baked potato, pineapples were thrown into the enclosure, the females would grab as much as possible and the males would get what was left or out of reach.

Individuals of differing rank did have a higher rate of socio-sexual behaviour, more so than individuals of the same rank and this supports the hypothesis that socio-sexual behaviour creates a social bond between individuals of different ranks. Interestingly in the Twycross group it was high ranked initiators with low ranked receivers that had the highest overall frequency. Low rank initiators had a more equal distribution of high and low ranked receivers, although slightly more high ranked receivers, and this suggests some kind of dominance interaction. Again, for the Planckendael group dominance hierarchy was not possible to identify and therefore initiation by rank was not known.

If dominance is the function, for bonobos, where females are the dominant sex, female/female socio-sexual behaviour would be expected to be far more frequent than male/male socio-sexual behaviour and this was very apparent. In both the Twycross and Planckendael groups male/male socio-sexual contact was extremely low and female/female socio-sexual behaviour extremely high, which was to be expected, although female/female socio-sexual behaviour in the Planckendael group was relatively lower in comparison to the Twycross group and one of the three adult females, Dzeeta did not participate in any same sex

socio-sexual behaviour. Male/male socio-sexual behaviour was relatively very infrequent but perhaps for different reasons in each group. In the Planckendael group the two adult males did not interact at all and juvenile and adolescent socio-sexual behaviour was the most frequent. The Twycross group males did interact and agonistic interactions were relatively infrequent, especially between the two adult males but socio-sexual behaviour was very infrequent and grooming appeared to be their main interaction.

4.91 Research under captive conditions and possible functions of socio-sexual behaviour

In order to show behaviour is adaptive, and to investigate what its function is, one has to investigate its contribution to the survival of an individual and reproduction. In a study made under captive conditions, like the present study, evidence can be collected about functional aspects of behaviour, but adaptiveness cannot be tested directly by studying increased evolutionary success under the conditions where the traits have evolved.

The function of socio-sexual behaviour has been investigated previously by Fruth (2000), Kano (1992), Furuichi (1992) and others under wild conditions. Five main functions were proposed for bonobos and chimpanzees (see pages 17-19), these are 1) conception, 2) practice, 3) paternity confusion (Hrdy 1981), 4) exchange and 5) communication and all apart from conception can be seen as socio-sexual behaviour for bonobos. De Waal (1990) suggested two further criteria for communication sex, that sexual contact is not a replacement for heterosexual sex, and that the sexual behaviour should be an integral part of 'normal' social life (1990, 1992). As we have seen this certainly was the case in his study. In a functional analysis of behaviour we need to consider the possibility that behaviour we investigate may not have evolved in relation to contributing to survival, but that it may be an artefact of unnatural circumstances, or an emergent property with no strong selective consequences. We have seen that the weight of evidence points towards beneficial selective

consequences for socio-sexual behaviour in bonobos, both in captivity as well as under natural conditions, and that these benefits may be in three areas. Apart from humans, only in bonobos is there evidence for communication sex; see also (Kano 1992, Kitamura 1989, Kuroda 1984). An example of such behaviour is GG rubbing by adult female bonobos, used extensively in many social contexts and in the presence of males.

4.92 Concluding remarks and comparison with humans

The evidence presented in this study suggests that socio-sexual behaviour has most probably evolved to 1) reduce tension and/or 2) to reaffirm dominance within bonobo groups. There is some evidence that also suggests social bonding. This latter function is supported by the finding that it is socio-sexual behaviour, such as GG rubbing, is particularly prevalent amongst adult females, and a bonding function amongst females is particularly important because females are unrelated, but the dominant sex in this species.

The evolution and function of human sexual behaviour between partners of the same sex has recently been re-analysed and reviewed by Kirkpatrick (2000). Based on the available evidence he concluded that homosexual behaviour in humans has evolved because of its nonconceptive benefits, i.e. communicative socio-sexual behaviour in the true sense, as social bonding (Kirkpatrick 2000:387). In humans heterosexual behaviour serves the same nonconceptive function, as well as for conception. Homosexual behaviour in this species aids same-sex alliance co-operation for defence or to assist in competing for resources like food. Therefore homosexual behaviour will have been positively selected for (Kirkpatrick 2000:388). Kirkpatrick distinguishes, behaviour based homosexuality with intention based homosexuality. He suggests that, if behaviour based, a comparison across species and cultures can easily be made, but that this is not easily possible if intentionality comes into the equation (Kirkpatrick 2000:389). If homosexual behavior has fitness benefits because of these same-

sex alliances, those alliances must help individuals in establishing and maintaining family units and, as a consequence, help any offspring survive to reproduce (Kirkpatrick 2000:393). There is ample support for this in humans (Kirkpatrick 2000:393). For example, in ancient Crete men were at a social disadvantage if they did not have a same-sex sexual partner (Boswell 1980), cited in Kirkpatrick (2000). Also in Melanesia, homosexual behaviour and female-exchange marriage link individuals and groups in mutual dependency and obligation (Lindenbaum 1984:345). This 'alliance formation' hypothesis suggests that exclusive homosexual behaviour is maladaptive, but 'self-motivated' homosexual behaviour enhances survival, therefore bisexuals would be expected to be more successful evolutionarily, compared to their exclusive heterosexual conspecifics. Kirkpatrick's findings that the vast majority of individuals who engage in homosexual behaviour, have heterosexual relationships also, supports this hypothesis (Kirkpatrick 2000:394).

It therefore appears that there may well be similarity and perhaps a level of homology between human and bonobo communicative socio-sexual behaviour. Bonding and alliance may be a function in both species. At the same time, it appears as though there are differences in this use of this behaviour also. In bonobos, same-sex alliances occur in both sexes, but more commonly between females whereas in humans it is a somewhat higher prevalence amongst males.

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